The macroecological distribution of avian functional diversity: environment, extinction risk and protected area coverage

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Abstract

134 bird have gone extinct since 1500 and more than a fifth are currently threatened or near-threatened. Consequences of biodiversity loss for ecosystems depend on community composition rather than simply species richness, hence interest in functional diversity (FD) - variety of traits that influence ecosystem functioning – has increased. This thesis uses a global set of avian traits and geographic range maps to investigate the macroecological distribution of FD. Old World latitudinal gradients of FD are found to reflect contemporary environment, particularly energy availability. Analyses restricted to sedentary species reveal the importance of migration (e.g. for breeding assemblages a positive association with temperature seasonality explains 6.7% of the variance in FD having accounted for species richness, whereas a negative association explains 21.4% for residents). This is further investigated by comparing seasons across the Palaearctic-Afrotropical flyway, e.g. functional richness (volume of trait space occupied by an assemblage), which ranges from 0 to 0.33, declines by 0.08-0.17 in the northernmost cells in the non-breeding season compared to the breeding season. Some traits increase sensitivity to human disturbance, e.g. habitat breadth, but birds across South and Southeast Asia are used to demonstrate scale-dependence; traits explain 21.4% of the variance in global extinction risk compared to 6.7% for local extinction with diet type more important in the former and use of manmade sites in the latter. Globally, narrow-ranging species are less likely to inhabit protected areas (12% of land surface) and analyses show they are associated with particular regions of trait space (those related to higher habitat strata, feeding at lower trophic levels and smaller body size) compared to better protected, wide-ranging species. By identifying the main environmental correlates of FD, factors associated with extinction risk and current FD protection, these findings could help identify areas at future risk of decreasing delivery of ecosystem processes.

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Chapter One: General introduction

1.1 Biodiversity can be measured in different ways

Biodiversity, the variety of life on Earth, is often treated as being synonymous with species richness (the number of species in a given area), but in reality it comprises variety at all levels of ecological organisation and includes "*diversity within species, between species and of ecosystems*" (UN, 1992). Ecosystem processes, including services vital to human life and health, depend on biodiversity (Loreau *et al.*, 2001; Hooper *et al.*, 2005), but biodiversity is currently being lost at rates far higher than natural extinction rates (Barnosky *et al.*, 2011) with ~30% of more than 70,000 species assessed by the IUCN threatened with extinction (IUCN, 2013). The large-scale spatial distribution of biodiversity across the world is heterogeneous (Gaston, 2000) and is a subject that has interested scientists since at least the 19th century. Alfred Wallace, who could be regarded as one of the earliest biogeographers, travelled extensively in South America and Asia. His experiences of tropical ecosystems led him to remark that "*animal life is, on the whole, far more abundant and more varied in the tropics than in any other part of the globe*" (Wallace, 1878). Latitudinal gradients in which biodiversity peaks around the equator and declines towards the poles have been described for a wide variety of taxa (Hillebrand, 2004). Understanding the causes of this and other large-scale distributions of biodiversity measures, as well as the consequences of biodiversity loss, are vital if we are to protect ecosystem processes.

Until recently, macroecological studies of biodiversity were mainly restricted to patterns in species richness (Gaston, 2000; see Figure 1.1). Species diversity, which is a function of both species richness and evenness, has been measured and investigated for decades in a variety of ways (e.g. Shannon, 1948; Simpson, 1949). However, increasingly ecologists are employing other means of quantifying biodiversity that utilise information on species' identities as well as their numbers. For example, consideration of the evolutionary relationships between species gave rise to phylogenetic diversity: the sum of the lengths of branches connecting species in a cladogram (Faith, 1992). Implicit in this definition is the suggestion that an ecosystem containing more distantly related species is more diverse than one in which its members are more recently diverged.

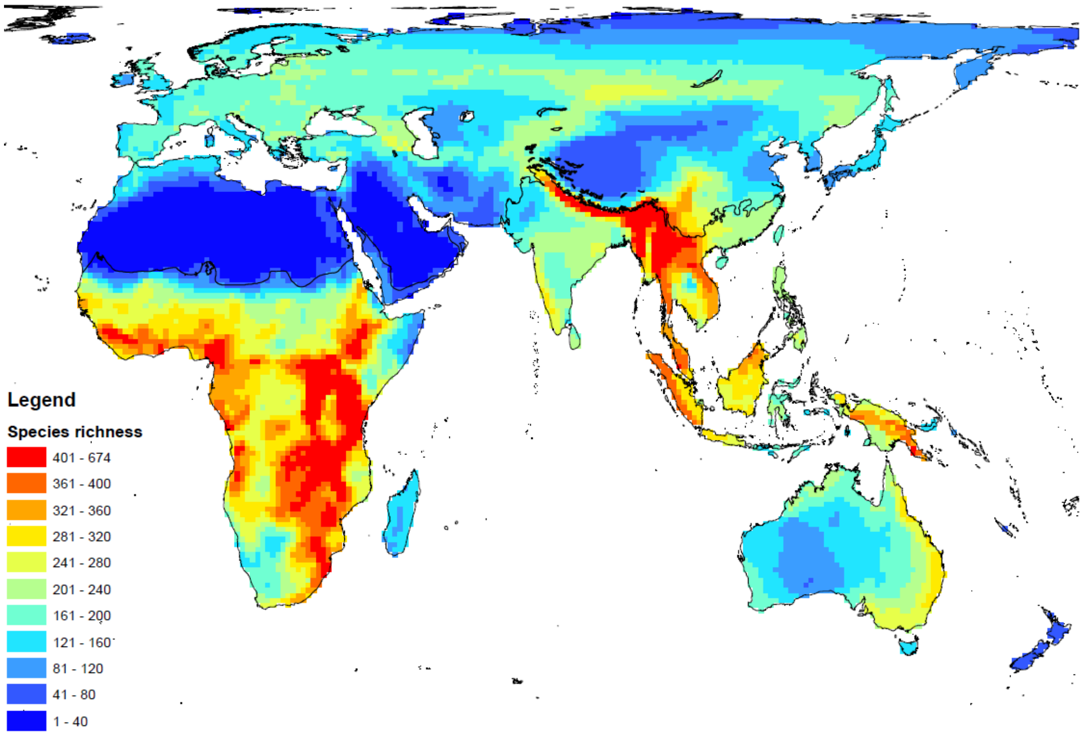

Figure 1.1: Distribution of bird species richness at 1-degree grid cell resolution across the Old World.

Relationships between species can also be characterised using traits related to their roles within an ecosystem and these functional relationships can be used to quantify functional diversity. There has been an increased emphasis on species' traits as ecologists have recognised that they can have a strong influence on the relationship between biodiversity and ecosystem processes (Loreau *et al.*, 2001; Petchey & Gaston, 2002; Hooper *et al.*, 2005). There have been many definitions of functional diversity from different authors – such as "*the functional multiplicity within a community*" (Tesfaye *et al.*, 2003), "*the distribution of the species and abundance of a community in niche space*" (Mason *et al.*, 2005) and "*the variability in the functional traits displayed by species in relation to a given set of ecologically relevant processes*" (Farias & Jaksic, 2009) – and it has been the subject of an increasing number of scientific papers since the 1990s (Cadotte *et al.*, 2011). The most widely-used and accepted definition is "*the value and range of those species and organismal traits that influence ecosystem functioning*" (Tilman, 2001).

Species, phylogenetic and functional diversity are interrelated and areas of high species or phylogenetic diversity may also have high functional diversity, but this is not always the case; hotspots of these three measures were found to have low spatial congruence for bird assemblages across France (Devictor *et al.*, 2010). Functional diversity does increase with species richness, but there is not always a linear relationship. For example, functional diversity of New World bats increases towards the equator at a greater rate than the increase in species richness (Stevens *et al.*, 2003). An ecosystem can have high species diversity and low functional diversity if the species present are functionally similar (Flynn *et al.*, 2009) and vice versa if species are particularly functionally dissimilar. Phylogenetic diversity is not equivalent to functional diversity since, although there is usually a high level of niche conservatism, closely related species may occupy rather different niches (divergent evolution) or there may be functionally similar species in an ecosystem that are not closely related (convergent evolution). For example, body mass variation (considered as a proxy for functional diversity since many important traits vary with body size) would be lost at a higher rate than phylogenetic diversity if currently threatened mammals went extinct (Fritz & Purvis, 2010).

1.2 Functional diversity can be measured in different ways

In order to measure functional diversity of a community, information on the constituent species and their functional traits is needed. This involves a number of decisions including which traits are relevant to include and how to record them. For example, a study on community assembly of plants included leaf phenology, leaf morphology and method of seed dispersal (Thompson *et al.*, 2009), while a study on arthropod responses to bird functional diversity incorporated foraging method, diet and body mass (Philpott *et al.*, 2009). In this thesis I have used traits related to resource use for birds (including body mass, diet and traits related to foraging), which involved the collation of data for species across the globe (9,052 species).

Functional diversity can be reported in terms of the number of functional groups present and the relative abundance of species in those groups (e.g. Arenas *et al.*, 2006). A criticism of the use of functional group richness is that there is subjectivity regarding group identity (Ricotta, 2005). Additionally, it assumes that all members of a group are functionally identical and interchangeable (Ricotta, 2005). Although the concept of functional group richness might seem intuitive, the process of calculation actually involves more steps and assumptions than do continuous measures of functional diversity (Petchey & Gaston, 2006). A bootstrap analysis, whereby data were reanalysed after random allocation of species to functional groups, has been shown to often provide results with higher explanatory power than analyses based on the *a priori* assignment of species to groups based on functional traits (Petchey, 2004).

In this thesis I have used continuous measures of functional diversity. The first step in each of these measures is to arrange the species in t-dimensional space, where each dimension represents a trait (Villéger *et al.*, 2008); species that occupy more similar niches (and have more similar traits) are closer together in this space. The ordination process can be used to identify which traits are most important in differentiating between species (e.g. Pease *et al.*, 2012; see Figure 1.1a) and to compare the position in space of species in different assemblages. The volume of trait space occupied and the regularity of species within the space can be used to calculate functional richness and evenness respectively (Mason *et al.*, 2005; see Figure 1.1b). An additional step is to use hierarchical clustering to group species according to similarity using the distances between them in trait space and to use these clusters to produce a functional dendrogram; species which are closer together in the trait space are also closer together on the dendrogram (see Figure 1.2c). Functional diversity is then calculated as the sum of the lengths of branches required to connect the species in a community (Petchey & Gaston, 2002; 2006). Consequently, when functional diversity is measured using a dendrogram, it is analogous to phylogenetic diversity.

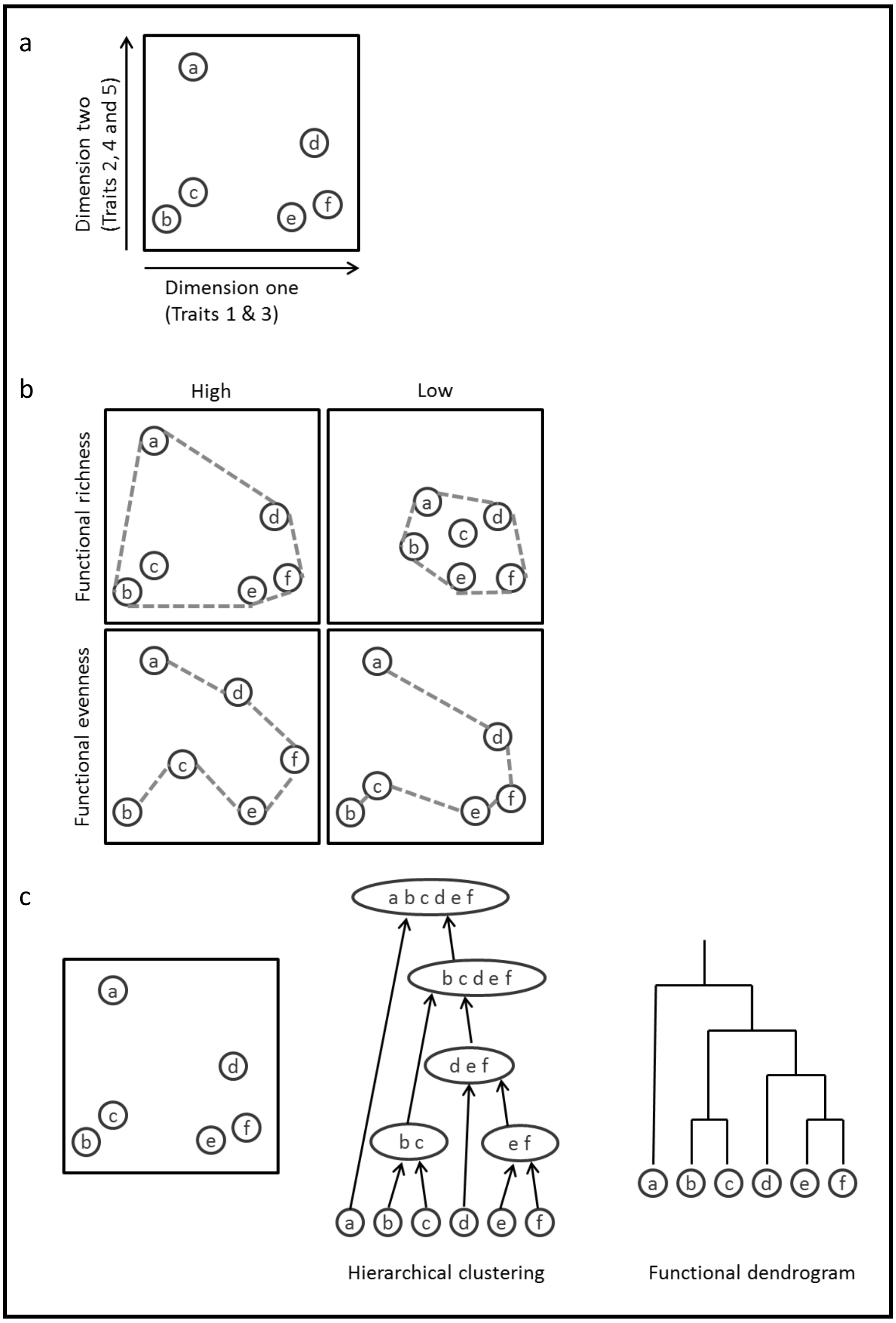

Figure 1.2: Ordination techniques are used to compare species' positions in multidimensional functional trait space. (a) In this case, traits 1 and 3 are most important in differentiating between species as they load onto the first ordination dimension. Species that have more similar traits are closer together, e.g. species 'b' and 'c' are more similar to each other than either is to species 'a'. (b) Functional richness is a measure of the volume of functional trait space occupied and functional evenness is a measure of the regularity of species within the space. (c) A matrix of the distances between species in trait space is subjected to hierarchical clustering in order to produce a functional dendrogram. Species which are closer together in the trait space are also closer together on the dendrogram.

Functional traits and their diversity have been used to investigate many ecological questions, including those related to community assembly (e.g. Petchey *et al.*, 2007; Mason *et al.*, 2008; Thompson *et al.*, 2009; Lebrija-Trejos *et al.*, 2010; Baraloto *et al.*, 2012) and to the impact of human-mediated biodiversity change and species extinctions (e.g. Tscharntke *et al.*, 2008; Flynn *et al.*, 2009; Vandewalle *et al.*, 2010; Edwards *et al.*, 2013).

1.3 Functional diversity can be used to investigate community assembly

Functional diversity has been used to investigate the support for different community assembly rules. Niche-assembly theory has been developed as an explanation of non-random processes contingent on the traits of the constituent species (e.g. Diamond, 1975; Keddy, 1992), whereas neutral theory assumes that all species are ecologically equivalent and that community assembly is random with regards to species' traits (Hubbell, 2001). Therefore, the assumptions of niche-assembly can be tested by comparing the distribution of functional diversity to the null distribution of species predicted by the neutral theory. Limiting similarity can increase trait dispersion and environmental filtering can cause trait clustering (Petchey *et al.*, 2007). Environmental filters may act at broader scales than biotic interactions (Díaz *et al.*, 1999), so a signal of environmental filtering mechanisms may be more evident in macroecological analyses.

A study of plant communities in NE Spain compared functional diversity within-communities (α-functional diversity) and the functional diversity among-communities (β-functional diversity) to null models (Bello *et al.*, 2009). They found that α-functional diversity was lower and β-functional diversity was higher than null expectation, i.e. each community was functionally quite different from one another, but species within communities were functionally quite similar. This lends support to environmental filtering at larger spatial scales; species are present in areas where the conditions suit their traits. Investigation of traits has shown that environmental filtering is also an important explanation of community assembly in a tropical dry forest (Lebrija-Trejos *et al.*, 2010), bird communities in Great Britain (Petchey *et al.*, 2007) and roadside plants in England (Thompson *et al.*, 2009). However, consideration of patterns of functional richness and evenness in lake fish communities in France provides evidence for the important role played by niche differentiation (Mason *et al.*, 2008). Functional evenness increased linearly with species richness, whereas functional richness was highest at intermediate levels of species richness. As species richness increased each species had a smaller niche space available, but niche overlap did not increase; instead, species' niches became more specialised (Mason *et al.*, 2008).

These theories are not necessarily mutually exclusive. Pacific rockfish provide evidence for the different processes being important at different spatial scales (Ingram & Shurin, 2009). At larger spatial scales, relative eye size is an important component of their β-niche (which describes species' response to environmental gradients) since it is related to the depth at which they can exist. At smaller spatial scales, their gill raker morphology is an important component of their α-niche (which describes local scale resource use) since it is related to trophic level. The authors showed that relative eye size was under-dispersed when compared with a null model, which supports the environmental filtering hypothesis at larger spatial scales, and gill raker morphology was less clustered than expected by chance consistent with the niche differentiation hypothesis at smaller spatial scales (Ingram & Shurin, 2009).

Furthermore, functional diversity may be lower than null expectations if there is higher species packing in trait space. It is thought that high species richness can result from finer niche partitioning (Hutchinson, 1959), so higher species packing is therefore associated with species having more similar trait values.

1.4 Functional diversity can be used to investigate consequences of biodiversity change and to prioritise conservation efforts

If species richness changes over time (e.g. as a result of extinctions or colonisations), functional diversity may change in unexpected ways. Knowing the relationship between species and functional diversity for a particular set of communities may help to predict the effects of community composition change (Flynn *et al.*, 2009). If there is high redundancy (i.e. a saturating relationship between increasing species richness and functional diversity), then the processes within that community may be preserved even with species loss. For example, functional diversity of bird communities in Great Britain indicates that there is little redundancy (Petchey *et al.*, 2007), which suggests that extinctions could have serious consequences. Even in communities with high redundancy, extinctions could affect ecosystem processes depending on which and how many species go extinct. Ehrlich & Ehrlich (1981) used the metaphor of a person popping rivets out of the wings of an aeroplane shortly before it is due to take off. The rivet-popper reassures the passenger that not all the rivets are necessary and that numerous rivets have already been removed without any serious consequences. Similarly, in communities with 'redundant' species, some may go extinct without seriously affecting ecosystem processes. However, although "*a dozen rivets, or a dozen species, might never be missed… a thirteenth rivet popped from a wing flap, or the extinction of a key species … could lead to a serious accident*" (Ehrlich & Ehrlich, 1981).

Extirpations due to anthropogenic effects such as habitat loss, hunting, introduction of invasive species and climate change are expected to bring about changes in efficacy of ecosystem processes (Hooper *et al.*, 2005). Extinctions may not be random losses and the order in which species go extinct can have different implications for ecosystem functions (Larsen *et al.*, 2005). Some traits may render species more vulnerable to threatening processes. Species might be more prone to extinction if they are large-bodied (e.g. Owens & Bennett, 2000; Sodhi *et al.*, 2004b; Peh *et al.*, 2005; Gaston & Blackburn, 1995), have a small altitudinal range (Lee *et al.*, 2005) or geographic range (e.g. Posa & Sodhi, 2006; Waltert *et al.*, 2004; IUCN, 2013), are insectivorous (Castelletta *et al.*, 2000; Thiollay, 1995; Waltert *et al.*, 2004; Zakaria *et al.*, 2005) or frugivorous (Thiollay, 1995), forage on the ground (Peh *et al.*, 2005), have specialised resource requirements (Sodhi *et al.*, 2005b), are long-distance migrants (BirdLife International 2013) or are long-lived (e.g. Webb *et al.*, 2002). Therefore, extinctions may lead to disproportionate losses of species with particular traits (e.g. Cardillo *et al.*, 2005) that affect ecosystem processes such as pollination (Potts *et al.*, 2010; Tscharntke *et al.*, 2008) or predation (Tscharntke *et al.*, 2008). Since species do not exist independently of one another, consideration of their interrelationships is essential in order to better predict the future effects of climate change (Gilman *et al.*, 2010) and other effects generating community change.

In a meta-analysis of data on species richness of plants, birds and mammals at different levels of agricultural intensification, it was found that bird and mammal functional diversity decreased with increasing intensification, whereas there was no clear pattern for plant communities (Flynn *et al.*, 2009). Of the bird and mammal communities in agricultural and semi-natural landscapes, 30.8% had a lower functional diversity than expected by chance for the number of species present (compared with 13.6% of natural landscapes). This means that the rate of functional diversity loss was higher in these communities than expected by chance and that simply monitoring species richness does not reflect the complete effects of species loss. For example, it has been shown that predicted extinctions of primates in Madagascar could lead to larger ecological changes relative to the projected taxonomic changes (Jernvall & Wright, 1998). The loss of functional diversity as a result of habitat disturbance is not irreversible. A study on ant diversity in tropical forests found that functional diversity increases as secondary forest is allowed to recover (Bihn *et al.*, 2010). The increase in functional diversity during the process of succession was mainly driven by the recruitment of rare species, which were more likely to be functionally unique.

The use of diversity metrics has been suggested as a way of prioritising areas for conservation (e.g. Myers *et al.*, 2000). Since hotspots of different aspects of biodiversity often show low spatial congruence (Myers *et al.*, 2000; Orme *et al.*, 2005; Stuart-Smith *et al.*, 2013), it is necessary to consider a suite of different diversity metrics to adequately conserve biodiversity in its broadest sense. Protecting areas of high functional diversity may preserve important ecosystem processes and could complement other priority areas, e.g. regions of high phylogenetic diversity (Stuart-Smith *et al.*, 2013).

1.5 Investigating biodiversity at macroecological scales can provide important insights

The term ‘macroecology’ was first used by James Brown and Brian Maurer in 1989 to describe a large-scale approach to understanding “*how the physical space and nutritional resources of large areas are divided among diverse species*” (Brown & Maurer, 1989). This top-down approach was partly a reaction to what they saw as the progressively more microscopic methodology being adopted by many ecologists, as well as an increasing need to consider ecological patterns and processes at continental scales because of the global nature of anthropogenic impacts on biodiversity (Brown & Maurer, 1989). This desire to see the bigger picture was described by Brown (1995) as “*not to understand a tapestry in terms of warp and woof and the chemistry of fibers and dyes, but to see and interpret the entire scene*” and by Gaston & Blackburn (2000) as a method that “*attempts to see the wood for the trees*”.

Macroecological approaches have been used to investigate ecological phenomena at continental to global scales such as the distribution of species richness (e.g. Orme *et al.*, 2005; Storch *et al.*, 2006; Davies *et al.*, 2007a; 2007b; Belmaker & Jetz, 2011), body size (e.g. Blackburn & Gaston, 1994; Olson *et al.*, 2009; Fritz & Purvis, 2010), geographic range size (e.g. Stevens, 1989; Orme *et al.*, 2006; Laube *et al.*, 2013), phylogenetic diversity (e.g. Davies *et al.*, 2007b; Fritz & Purvis, 2010) and, more recently, species’ traits (e.g. Safi *et al.*, 2011;

Belmaker *et al.*, 2012). Although macroecology has provided many insights into large-scale patterns of biodiversity, it has been more difficult to identify the processes underlying those patterns. As advocated by Brown (1999) a decade after the original paper outlining the field of macroecology, there are now increasing efforts to understand the drivers of macroecological patterns (Keith *et al.*, 2012; Beck *et al.*, 2012), although in the past it has necessarily been a largely correlative approach (Gaston & Blackburn, 2000).

1.6 Birds are an ideal model system for investigating the macroecological distribution of biodiversity

Birds are often chosen for macroecological analyses since they are one of the most well-studied taxa (Kent, 2005); less than 1% of bird species are listed as being data-deficient (IUCN, 2013). This thesis addresses the distribution of functional traits across the globe and as such involved the collation of tens of thousands of trait values, most of which were collated from handbooks. The publication of the Handbooks of the Birds of the World took nearly two decades (Volume one: Ostrich to ducks, Del Hoyo et al., 1992; Volume sixteen: Tanagers to New World blackbirds, Del Hoyo et al., 2011) and illustrates why birds are an ideal taxonomic group for these analyses. The volumes, which contributed a large proportion of the data used for the analyses of functional diversity in this thesis, are the first ever works to provide written descriptions and illustrations of an entire class of Animalia and contain a huge quantity of data contributed by ornithologists from across the globe, with a total of 12,564 pages and a combined weight of 67 kg (Garrett, 2012)! When performing macroecological studies, it is important to take into account potential spatial biases in data quality. For example, range maps will be more accurate in regions where accessibility and proximity to research stations mean that greater sampling effort has been applied and more reliable data have been collected (Rocchini *et al.*, 2011). However, the macroecological patterns of bird communities have been shown to be robust to differences in data quality (Mathias *et al.*, 2004).

As well as being well supported by data sources, birds are also an interesting model system since they contribute important ecosystem services. Şekercioğlu (2006) identified that birds are particularly important for regulating services (including seed dispersal, pollination, pest control and carcass and waste disposal) and supporting services (including nutrient deposition and ecosystem engineering). These services may be at risk as a result of population declines and extinctions (Şekercioğlu *et al.*, 2004).

1.7 Thesis structure

In this thesis, a database of functional traits for birds across the globe (9,052 species) and maps of species' ranges are used to investigate the distribution of functional traits and their diversity at macroecological scales. I use these data to explore: (1) environmental influences on the large-scale distribution of avian functional diversity and occupancy of functional trait space and (2) how this is different for endemic and widespread species; (3) how the distribution of functional diversity is affected by seasonal change in community composition as a result of migration; and (4) what traits are associated with the threat of local extirpation and global extinction and their relative importance compared to extrinsic factors.

Although latitudinal gradients have mainly been described for species richness of various taxa, less is known about the large-scale distribution of functional diversity. In **Chapter two**, I map the distribution of functional diversity (measured using a functional dendrogram; Figure 1.2c) across the Old World (5,191 breeding bird species). I also compare the distribution of observed functional diversity to null expectations (i.e. that expected if assemblages are random with respect to species' traits). Although there is still debate about the relative importance of different environmental drivers of large-scale patterns of biodiversity distribution, there is wide support for the roles of energy and of habitat heterogeneity (see Figure 1.3); there are more species in areas of higher temperatures, greater productivity and/or a greater range of habitats (Evans *et al.*, 2005; Davies *et al.*, 2007a). Using spatial regression models (to account for spatial autocorrelation, or the non-independence of data due to the tendency for points close in space to be more similar than points further apart), I test these variables and other climatic and anthropogenic factors to identify the most important predictors of the distribution of functional diversity (both absolute values and those relative to null expectation).

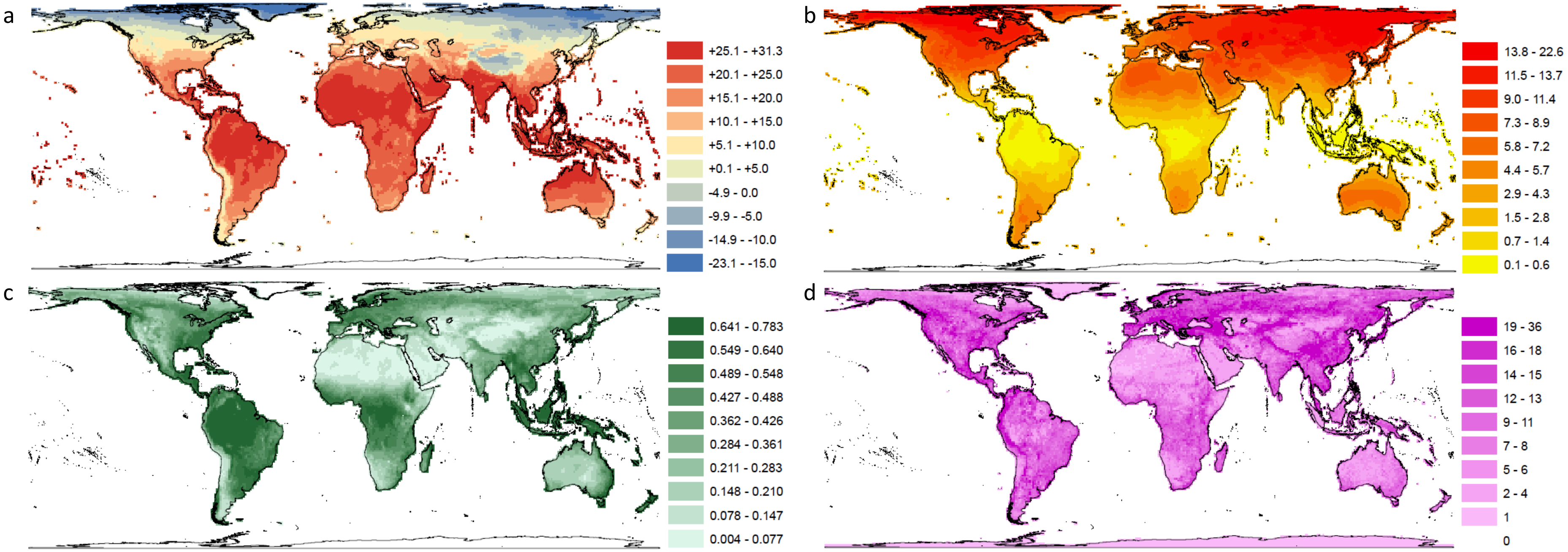

Figure 1.3: Possible environmental drivers of global latitudinal patterns of biodiversity distribution. The role of energy can be tested using ambient measures including mean annual temperature (°C) (a) and its seasonality (standard deviation) (b), or productive energy measures such as NDVI (c). The role of habitat heterogeneity can be tested using measures including the number of different habitat types (d).

I expand upon the findings from the first chapter by mapping the distribution of functional richness and the use of trait space across the Old World in **Chapter three**. I use multivariate methods to measure and investigate these concepts. Firstly, principal coordinates analysis (an ordination technique suitable for data that includes traits measured on a continuous scale) is used to visualise species in trait space (Figure 1.2a) and to identify which traits are most important in distinguishing between species' functions. Secondly, the volume of the convex hull of species in trait space is a measure of functional richness (Figure 1.2b). I then use the same spatial regression techniques to investigate whether the same variables that I found to be important in predicting the distribution of a dendrogram-based measure of functional diversity are also good predictors of functional richness and the use of trait space. These analyses provide insight concerning mechanisms underlying the latitudinal diversity gradients.

In both of the first two chapters, I use breeding distributions of species to compile assemblages of species across the Old World. I compare the results when all breeding species are included to those with resident species only (i.e. excluding migratory species). Migratory bird species avoid severe winter conditions at high latitudes by spending their non-breeding season at lower latitudes and are therefore not under the same selection pressures as sedentary species at high latitudes (Stevens, 1989), which may also be more dispersal-limited (Paradis *et al.*, 1998). Therefore, it is perhaps not surprising that some contrasting results are revealed when analyses are restricted to sedentary species.

In order to further explore the effect of seasonal community change on functional diversity, in **Chapter four** I compare the functional richness and evenness (Figure 1.2b) of assemblages in the breeding and non-breeding season in one of the main migratory routes: the Palaearctic-Afrotropical flyway (2,310 bird species). I also compare the dissimilarity of assemblages in terms of their taxonomic dissimilarity (i.e. species turnover) and functional dissimilarity between the two seasons. North of approximately 40°N, species richness is substantially higher in the summer breeding season compared with the more physiologically-demanding winter months (Somveille *et al.*, 2013). However, it is not yet known whether this pattern is reflected in seasonal changes in functional diversity. This in part depends on the position of migratory species in trait space when compared with resident species.

The latter two chapters of the thesis investigate the impact of human-mediated biodiversity change on species' traits and consider the possible effects of species extinctions on functional diversity. In **Chapter five**, I identify which traits are associated with being sensitive to local disturbance (e.g. agricultural conversion) and which traits are associated with being globally threatened (using IUCN Red List status) for birds in South and South-East Asia (1,996 species). I also compare their relative importance with extrinsic factors such as land-use change. I use predicted relationships with traits associated with local sensitivity to identify species which are currently of Least Concern, but which may become threatened if extrinsic factors change within their range, e.g. if a greater proportion of natural habitat is converted to a human-dominated landscape.

Conserving species can be achieved in many different ways, one of which is through the Protected Area Network which currently covers more than 12% of the world's land surface (Jenkins & Joppa, 2009). Species are more likely to occur within a protected area if they have a large geographic range; endemic species are under-represented (Rodrigues *et al.*, 2004b). In **Chapter six**, I use a complete global set of bird species (9,052 species) to investigate whether a species' position in trait space varies with range size and therefore whether traits associated with small range size are not adequately protected. I also map the distribution of functional richness of endemic and widespread species to identify areas where narrow-ranging species may be of particular importance for ecosystem processes.

Finally, in **Chapter seven** I draw some general conclusions from across the thesis.

Chapter Two: Productivity and temperature seasonality predict functional diversity of Old World bird assemblages

2.1 Abstract

Aim: To map the large-scale distribution of avian functional diversity (FD) across the Old World (5,191 species). To use null models to assess large-scale variation in environmental filtering. By comparing breeding assemblages with residents only, to gain a more mechanistic understanding of avian latitudinal diversity gradients. To investigate the influence of key environmental and anthropogenic gradients upon these patterns.

Location: The Old World (Palaearctic, Indo-Malaya, Afrotropics and Australasia).

Methods: We used a dendrogram method to estimate the distribution at a 1-degree resolution of FD and the Standardised Effect Size (SES_{FD}: calculated as the difference between the observed FD and the FD expected (FD_{exp}) by randomly drawing the same number of species from the regional species pool, and dividing this difference by the SD of FD_{exp}). The most important predictors were identified using spatial regression models and hierarchical partitioning.

Results: Distribution of FD strongly resembles that for species richness with which it is highly correlated. In contrast, highest values of SES_{FD} are found in India, eastern China and southern Africa while lowest values occur in Sundaland and high northern latitudes (residents only). Biogeographic realm was very important in explaining the large-scale distribution of FD (explaining 13.9% of the variance in FD), and the most important variable in explaining SES_{FD} (explaining 57.1% and 36.0% of the variance in SES_{FD} for all breeding species and residents respectively), across the Old World. Of the continuously measured variables, those associated with productive energy were the strongest predictor of FD (and species richness) – precipitation explained 14.3% of the variance in FD and NDVI explained 13.0% – while mean temperature and its seasonality were the most important predictors of SES_{FD}, explaining 10.0% and 6.7% of the variances in SES_{FD} respectively. Relationships with predictors varied when only residents were considered, e.g. temperature seasonality showed a positive relationship with SES_{FD} for breeding assemblages, but negative for residents (while also explaining a much greater proportion of variance – 21.4%).

Main conclusions: The latitudinal gradient in species richness is best explained by productive energy, but FD signals greater importance of temperature seasonality. The differences in the association of environmental predictors with SES_{FD} for all breeding species and for residents only, suggest that future changes in the distribution and abundance of migratory species could have profound effects on FD in some regions.

Keywords: Community assembly, ecosystem processes, environmental filtering, functional traits, limiting similarity, null model, Old World, species packing.

2.2 Introduction

The environmental drivers of large-scale patterns of biodiversity distribution, and the underlying mechanisms with which they are associated, continue to be the subject of much debate. While variants of the energy and habitat heterogeneity hypotheses have both received widespread empirical support in explaining species richness distribution (Evans *et al.*, 2005; Davies *et al.*, 2007a), there are limits to gains in mechanistic understanding from species richness studies alone. Hence, alternative biodiversity metrics (e.g. functional diversity, Safi *et al.*, 2011) are increasingly used to gain a better understanding of latitudinal diversity gradients and their functional ecological significance.

Functional diversity (FD) is a measure of the variety of ecological roles represented by the species present in an ecosystem. As such FD takes account of levels of species complementarity within assemblages (Petchey & Gaston, 2002), hence is a more appropriate response variable for the testing of niche-based hypotheses. Although FD and species richness are likely to be strongly inter-correlated at macroecological scales, differences in their relative strengths of association with environmental drivers could be mechanistically revealing. Moreover, null model methods for understanding large-scale variation in FD by controlling for the contribution of species richness may provide mechanistic insights. Using this approach, observed values of FD (FD_{obs}) are compared with null expected FD (FD_{exp}) using random draws of equal species richness from the regional species pool. Such null models draw upon neutral theory that all species are ecologically equivalent (Hubbell, 2001). Greater than expected trait dispersion (high FD) is usually interpreted as the influence of biotic interactions such as competition (limiting similarity) while greater than expected clustering of traits (low FD) can be interpreted in two ways: in areas of low species richness it is thought to be the result of environmental filtering (Petchey *et al.*, 2007); in areas of high species richness it indicates finer niche partitioning (Hutchinson, 1959) and greater species packing.

Environmental filtering and biotic interactions are not mutually exclusive processes (Laliberté *et al.*, 2013). However, their relative influences are thought to vary with the spatial scale at which community assembly studies are conducted. Studies of bird assemblages reveal that the scale at which biotic interactions can be detected may be many orders of magnitude greater than the scale of individual territories at which they are more typically considered to operate (Gotelli *et al.*, 2010). Nevertheless, habitat filters tend to act at larger scales than biotic interactions (Díaz *et al.*, 1999), hence a signal of environmental filtering mechanisms may be more evident in macroecological analyses. The issue of scale should inform the choice of null model, or more specifically the regional species pool used to implement it, since the latter is well known to influence the outcome of analyses (Schoener, 1988). While studies at more local scales typically need to factor out the larger-scale influence of habitat filtering in order to detect biotic interactions (e.g. De Bello *et al.*, 2012; Laliberté *et al.*, 2013), variation in the intensity of environmental filtering across latitudinal diversity gradients is itself a subject worthy of investigation. In broad terms, the influence of environmental filtering can be predicted to vary with latitudinal variation in climate regime, biomes, and the extent and intensity of anthropogenic influences. The signatures of these environmental drivers upon contemporary FD distribution may reflect both long-term historical as well as more recent contemporary influences.

Species-energy theory can be considered with reference to two alternative energy variants, ambient (or solar) energy (Currie, 1991) and productive energy (Wright, 1983; Waide *et al.*, 1999). The mechanisms proposed to underpin species-energy relationships have been comprehensively reviewed elsewhere (e.g. Evans *et al.*, 2005) and, as species richness is strongly positively associated with FD, FD-energy relationships can be expected to broadly reflect the shape of species-energy relationships. Nevertheless, some differences can also be predicted, in light of mechanisms associated with the productive energy hypothesis. Increase in productive energy is predicted to be associated with an increase in the abundance of individual resource types, enabling consumers to specialise on preferred resources and resulting in a decrease in average niche breadths (Evans *et al.*, 2005). This in turn means that accumulation of FD should decelerate more rapidly with increasing productivity compared with species accumulation. We can therefore predict weaker FD-energy relationships compared with species-energy relationships, and analyses of FD that control for species richness should find negative FD-energy associations. In contrast, the range limitation mechanism thought to underpin the ambient energy variant of the energy hypothesis, proposes that increase in solar energy brings climates within the eco-physiological tolerances of a greater number of species (Evans *et al.*, 2005). Arguably, this works partly through relaxation of constraints on ecophysiological traits such as body size and morphology, with consequences for total available niche space and FD. However, direct consequences for average niche breadth are not obvious. In European fish communities, areas with harsh environmental conditions (extreme temperatures and low precipitation) had lower FD (Schleuter *et al.*, 2012).

Recent studies highlight the need for species-energy theory to take greater account not just of mean annual energy but of the potential role of energy seasonality in influencing species richness (Carrara & Vázquez, 2010). Both seasonality of climate and of resource availability are predicted to drive increased niche breadth (Evans *et al.*, 2005). Population numbers of permanent residents in particular are predicted to be constrained by seasonality of resources more than by mean annual levels of resource availability (Carrara & Vázquez, 2010). Migrants on the other hand are likely to complicate seasonality-richness relationships since they contribute to species richness during summer breeding seasons in highly seasonal environments and during non-breeding seasons to species richness in less seasonal environments. We predict that high seasonality of resources will be associated with low overall FD but relatively higher FD than expected for the number of species present, especially for residents. Temperature seasonality on the other hand is likely to have a strong filtering effect on the traits of species that are resident, and little effect on summer breeding migrants.

Climate variability impacts on biodiversity are also likely to have a historical component (Araújo *et al.*, 2008). Hence, recent studies have increasingly used a combination of contemporary ecological and historical predictors to explain the distribution of biodiversity. Davies *et al.* (2011) found that contemporary climate and temperature change since the last glacial maximum (LGM) are both important in explaining the global distribution of mammal species richness. Within a taxonomic group, the relative importance of contemporary and historical conditions may be different for particular subsets of species. A recent study using measures of horizontal climate velocity that capture the mitigating effect of topographic variability on rates of historical temporal climate change revealed that levels of species endemism decrease with increasing climate velocity (Sandel *et al.*, 2011). Given the association between species range size and niche breadth (Slatyer *et al.*, 2013) it could be expected that spatial gradients of increasing climate velocity would be associated with decreasing total FD and increasing FD controlling for species numbers.

The widely reported negative anthropogenic impacts on biodiversity from land-use include numerous examples for FD (e.g. Flynn *et al.*, 2009; Edwards *et al.*, 2013). Studies accounting for species numbers reveal a range of FD responses from negative (underdispersed) to positive (overdispersed). Nevertheless, underdispersion of FD appears to be the most frequently observed outcome. A meta-analysis found that for some communities of birds and mammals, FD (calculated using resource acquisition traits) decreased with increasing agricultural intensification at a greater rate than the loss of species numbers, suggesting that functionally distinct species were more likely to be lost as a result of agricultural intensification than functionally similar species (Flynn *et al.*, 2009). However, agriculture is not always negatively associated with FD; high regional bird FD in France was associated with a high % of meadows and annual agriculture (Meynard *et al.*, 2011). Bird assemblages have also been shown to have lower FD in logged forest and oil palm plantations than in unlogged forests (Edwards *et al.*, 2013). This loss of FD in human-modified landscapes could be indicative of biotic homogenisation (Mckinney & Lockwood, 1999).

In this study, we map the large-scale distribution of total FD for all breeding and resident bird species across the Old World (Palaearctic, Afrotropics, Indo-Malaya and Australasia). To better assess the influence of environmental filtering across avian latitudinal diversity gradients, we investigate how avian FD varies geographically from null expectations (given species richness), and contrast this FD pattern with the same for resident species only. We go on to compare the strengths and directions of associations of key climatic, habitat and anthropogenic drivers of FD and species richness distribution, taking account of their historical influences where data allow. In doing so we test the climatic/energy hypotheses outlined above and the prediction that anthropogenic impacts contribute to filtering effects on FD. Gains in mechanistic understanding of the avian latitudinal diversity gradient and implications for future global change are discussed.

2.3 Methods

2.3.1 Distribution of bird species

Analyses of bird species distributions were carried out using ArcMap 9.3 (ESRI, 2010). Shape-files of species' ranges were provided by BirdLife International (Birdlife International & Natureserve, 2011). These polygon maps are based on known locations (e.g. geo-referenced point locality records, collecting locality of museum specimens) and expert opinion (see Buchanan *et al.*, 2011 for details). For each species, the areas in which it is considered extant or probably extant throughout the year and those in which it is present only in the breeding season were included separately and areas where it was considered possibly extant or possibly extinct or where its presence was uncertain were excluded. Sea birds, defined as those species that predominately feed at sea and are described as pelagic or feeding offshore (Del Hoyo *et al.*, 1992; 1996), were excluded from the analysis (58 species). The exclusion criteria were consistent with those used in other macroecological analyses of bird distributions (e.g. Orme *et al.*, 2006). Migratory bird species that breed at high latitudes avoid severe winter conditions and are not under the same selection pressures as birds that remain resident year-round (Stevens, 1989). In addition, resident birds are on average more dispersal-limited (Paradis *et al.*, 1998), hence we predict that their patterns of diversity carry a stronger signal of historical environmental processes. Therefore, analyses of FD controlling for species richness were conducted on two sets of species: all bird species present in the breeding season (breeding visitors and resident species); and resident species only. Non-residents were not analysed in isolation, since they are only present in the company of residents and in some areas may make up a relatively small proportion of the overall species richness.

The range maps of birds present in the Palaearctic, Afrotropical, Indo-Malayan and Australasian realms (Olson *et al.*, 2001) were sampled on a grid using the Behrmann cylindrical equal-area projection. The cell resolution was 96.486 km x 96.486 km, equivalent to a 1° longitude and 1° latitude grid at the 30° latitude of true scale. This created 9,856 assemblages across the four realms where grid cells had >50% land area; each assemblage comprised all those species whose ranges overlapped with the grid cell.

2.3.2 Trait data

For our estimates of bird assemblage FD, we selected traits related to resource use (Table 2.1). Feeding location, strata used and diet were considered as binary traits since the categories are not exclusive e.g. a bird could feed both on the ground and in vegetation. Trait values for each species were collated using a variety of sources (listed in Appendix S1: Sources used for bird trait data). Where data were not available for individual species (<10% of species-trait combinations), genus, or failing that family, values were used (Table 2.1): 14.5% of species were assigned values for one trait using the genus average and 15.3% of species were assigned values for more than one trait using the genus average; 3.1% of species were assigned values for one trait using the family average and 1.1% of species were assigned values for more than one trait using the family average. Overall, 90.7% of the species-trait combinations used were specific to individual species, 8.4% were genus averages and 0.9% were family averages.

Table 2.1: Functional traits used for calculating functional diversity.

Trait		Possible values	% Species-trait combinations using averages	
			Genus	Family
Weight ($\log_e$ grams)	Continuous	1.61-11.62	9.7	1.0
Circadian activity	Categorical	Diurnal / nocturnal / crepuscular / all times	10.1	2.3
Feeding group size	Ordinal	1 / 2-6 / 6-10 / 10-20 / 20-50 / >50 individuals	9.2	0.9
Feeding location(s)	Ground	Yes / no	6.3	0.3
	Water	Yes / no		
	Vegetation	Yes / no		
	Aerial	Yes / no		
	On other animals	Yes / no		
Strata used	Ground/water	Yes / no	8.9,	0.8,
	Grass/low vegetation	Yes / no	10.2*	0.8
	Shrub layer/understorey	Yes / no		
	Mid-storey	Yes / no		
	Canopy or above	Yes / no		
Diet	Vertebrates	Yes / no	4.7	0.2
	Invertebrates	Yes / no		
	Fruit & berries	Yes / no		
	Seeds & nuts	Yes / no		
	Nectar & sap	Yes / no		
	Foliage & other plant parts, e.g. roots	Yes / no		

*Genus averages were used for 8.9% of species for the highest stratum used and 10.2% for the lowest stratum; species are assumed to use all the strata in between their highest and lowest heights.

2.3.3 Functional diversity

The functional diversity metric chosen was Petchey and Gaston's (2002; 2006) FD, which varies continuously between 0 and 1 (even when the traits used are not all continuous). This metric measures the distribution of species in functional trait space and as such is a measure of functional richness (Petchey & Gaston, 2006). A functional dendrogram was computed from a matrix of pairwise distances between species based on their traits and a Gower distance measure, which is suitable for traits not measured on a continuous scale (Gower, 1971). The lengths of branches required to connect all the species in each cell were calculated, with the assumption that summed branch length is positively correlated with FD (Petchey & Gaston, 2002; 2006). The unweighted pair-group clustering method using arithmetic averages (UPGMA) was chosen since it produced the highest cophenetic correlation (Blackburn *et al.*, 2005) compared with single linkage and complete linkage. The cophenetic correlation is a measure of how well the species distances are conserved in the functional dendrogram compared with the distance matrix (the correlation of pairwise distances on the dendrogram and the pairwise distances in the matrix).

2.3.4 Null models

Since the addition of new species to a community can only cause FD to increase or not change, FD is positively correlated with species richness (Petchey & Gaston, 2002). Additionally therefore, we derived FD controlling for species numbers, by subtracting FD expected from a null model (FD_{exp}) from observed FD (FD_{obs}). For our null models we randomly selected from the regional species pool the same number of species as present in a given cell, with the probability of a species being selected being proportional to the number of cells in which it was present (i.e. its occurrence), to ensure that rare species did not have a disproportionate influence (Mendez *et al.*, 2012). Since the choice of regional species pool has an influence on results, we tested two alternative regional pool definitions to ensure that our results were robust. In the first case, the regional pool for a given cell corresponded to the species present in the biogeographic realm in which the cell was located. Hence, there were 1860 species for cells in the Afrotropics (1835 for residents), 1435 (1419) for Australasia, 1727 (1620) for IndoMalaya and 1603 (1233) for the Palaearctic. In the second case, the regional pool used for all cells included all bird species present in the Old World. In both cases, the FD of the simulated community was calculated and this was repeated 100 times for each cell, the mean FD of these randomisations being the expected functional diversity (FD_{exp}). The difference between FD_{obs} and FD_{exp} (FD_{obs} minus FD_{exp}) was then calculated and divided by the standard deviation of FD_{exp} to calculate a standardised effect size (SES) (Gotelli & Mccabe, 2002). This ensures that differences between FD_{obs} and FD_{exp} are directly comparable for cells with different species richness. Since both ways of defining the regional pool gave broadly similar results, those resulting from the old World regional pool are reported in the supplementary material. Computation of FD and all statistical analysis was carried out using R version 2.12.0 (R Development Core Team, 2010).

2.3.5 Explanatory variables

The explanatory variables chosen are summarized in Table 2.2. The data for the candidate predictors were reprojected and resampled to the same equal-area projection and resolution as the species range maps. We included land area of each grid cell as a covariate in all models to control for species-area effects. Biogeographic realm was included as a factor to take account of potentially large biogeographical differences between the four realms in a given response variable that are not accounted for by our environmental predictors. In this context, realm may represent a surrogate index of different biogeographic histories (Schluter & Ricklefs, 1993) and could also capture contemporary environmental variables not tested using the contemporary predictors.

Contemporary climate was considered in two alternative ways: annual means (temperature and NDVI) or annual totals (precipitation) versus annual seasonality of temperature, precipitation and NDVI (Carrara & Vázquez, 2010). Temperature and precipitation data were from the 2.5’ WorldClim climate dataset (Hijmans *et al.*, 2005). We used mean annual remotely sensed NDVI for the period 1982-1996 at 0.25° resolution from the International Satellite Land-Surface Climatology Project (ISLSCP, 2005). Historical climate change was represented by the velocity of temperature and precipitation since the LGM. The velocity of a climate variable at a given location is equivalent to the speed at which a species would need to move in order to remain in constant climatic conditions. For a given climate variable, horizontal velocity is calculated as the amount of change in that variable over time (anomaly) divided by its spatial gradient; consequently, areas of greater topographical variability experience lower climate velocity, hence their constituent species need to move a shorter distance (i.e. up or down a mountain) to track change in climate (Loarie *et al.*, 2009).

Table 2.2: The potential predictors of functional diversity at the macroecological scale considered in this and the next chapter (LGM = last glacial maximum).

		Contemporary	**Historical**
Environmental	Absolute	Mean annual temperature(-20.4-30.2°C) Total annual precipitation (0-5252.5mm) Mean annual NDVI (0.02-0.78)	
	Variability	Temperature seasonality (standard deviation) (0.18-22.6)	Temperature change velocity since LGM (3.5-1033.3 km since LGM)
		Precipitation seasonality (coefficient of variation) (0-229.0)	Precipitation change velocity since LGM (0-2.7 km since LGM)
		NDVI seasonality (|October–March mean minus April–September mean|) (0-0.46)	
	Heterogeneity	Habitat heterogeneity - number of landcover types (1-36)	
Anthropogenic	Population	Human population density in 2000AD (0-3066 persons km^{-2})	Median arrival time of anatomically modern humans (500-80000 years)
	Agriculture	Cropland extent in 2000AD (0-9205 km^{2})	Period since conversion to cropland (0-10010 years)
		Pastureland extent in 2000AD (0-9310 km^{2})	Period since conversion to pastureland (0-7010 years)

To account for the potential influence of contemporary habitat heterogeneity on SES_{FD}, via effects of habitat turnover (Whittaker, 1960), we used the number of landcover types (Olson *et al.*, 2001) rather than topographic variability (maximum minus minimum elevation). The former is estimated from contemporary landcover maps, while the latter variable cannot be considered unequivocally contemporary since topographic variability has changed little since the LGM (e.g. Schuldt & Assmann, 2009).

Among our descriptors of contemporary anthropogenic effects, we included human population density (persons km^{-2}). In accounting for the influence of agricultural land-use we tested the fit of cropland and pastureland separately, using the contemporary areal extent (km^{2}) of each (Klein Goldewijk et al., 2011). This decision was based on the expectation that these two agricultural land uses affect community composition differently. Firstly, they can provide different resources for birds; granivores might be more attracted to cropland because of the availability of crop seeds and insectivores have been shown to prefer feeding on pastureland because they provide the highest abundance of soil macro-invertebrates (Tucker, 1992). Secondly, they have different kinds and intensities of impacts on biodiversity, with cropland likely to be more modified relative to natural ecosystems than pasturelands (Ellis, 2011). A study of birds in the UK demonstrated that farmland bird species are unlikely to be agricultural generalists, but are instead associated with one or two agricultural landscape types (Atkinson et al., 2002). Historical anthropogenic effects were represented by the time since median arrival of anatomically modern humans (Eriksson et al., 2012) and the duration of time since conversion (years) to pastureland and cropland (Klein Goldewijk et al., 2011). Further details on the data used for environmental and anthropogenic drivers are available in Appendix S2: Further information on data used for environmental and anthropogenic drivers in chapters two and three.

Bi-plots of the predictors were inspected and the variance inflation factors (VIF) calculated to assess levels of collinearity. Since each of the VIF values was <10 (Quinn & Keough, 2002), all predictors in Table 2.2 were considered in model selection. All predictors were z-standardised. The following variables were transformed because they showed right-skew: total precipitation and NDVI seasonality were square-root transformed and temperature change velocity, precipitation change velocity, human population density, cropland extent and pastureland extent were log$_{10}$-transformed. Plots of all variables against SES_{FD} were inspected to identify obvious non-linearities. As a result, the fit of square terms was tested for the following variables: temperature, temperature seasonality, precipitation seasonality, cropland duration and pastureland duration. Resampling of all environmental and anthropogenic data was carried out in SAS version 9.2.

2.3.6 Environmental models

We analysed the environmental predictors of FD_{obs}, species richness, and SES_{FD} using simultaneous autoregressive (SAR) models in order to control for the effects of spatial autocorrelation on model inference (Haining, 2003; Bivand, 2006; Kissling & Carl, 2008) since OLS residuals showed autocorrelation (see correlogram in Appendix S3). Spatial error models (SAR_{err}) were used, which account for spatial autocorrelation in model residuals by adding a spatially-dependent error term to Ordinary Least Squares (OLS) regression models. This method was chosen because SAR_{err} effectively reduces spatial autocorrelation, shows good precision in parameter estimates and good Type I Error control (Kissling & Carl, 2008). By using a neighbourhood distance of 1.5 cells, each cell had up to 8 neighbours (i.e. any cells that share a border or vertex) and the spatial weights matrix was row-standardised. Using these attributes, Moran's I of the residuals of the SAR_{err} model was close to zero at all distances, indicating that the residual autocorrelation was successfully removed (see correlogram in Appendix S3: Accounting for spatial autocorrelation).

Single-predictor models of each variable (with land area as a covariate) were built to check the strength and direction of individual relationships. To test the relationships with squared terms, the linear term was also included in the model. Starting with a full model that fitted all predictors (Table 2.2) we used backwards removal (based on improvement of AIC) to arrive at a minimum adequate model (MAM) with the lowest AIC. Squared terms were only included in models where the linear term was also present. Land area and biogeographic realm were fitted in all models. We used hierarchical partitioning to establish the relative importance of the predictors in the MAM. Since this method cannot be used with SAR models, we first removed the spatial component of the fitted values to create a new response variable. This new response variable was used in an OLS regression and we then performed hierarchical partitioning (Belmaker & Jetz, 2011). The results therefore indicate the importance of predictors in explaining the variance that is not attributed to the random spatial component. Hierarchical partitioning was carried out using the 'lmg' metric in the calc.relimp function of the relaimpo package (Groemping, 2010) of R.

2.4 Results

Our results confirm that FD is highly correlated with species richness (Figure 2.1a) while SES_{FD} is only very weakly correlated with species richness (Figure 2.1b). Hence, large-scale distribution of FD (Figure 2.2a) closely resembles that for species richness (see Supplementary Figure 2 in Appendix S4), e.g. highest FD in the Himalayas, East African Rift and Eastern Australia (Figure 2.2a). The majority (72.1%) of grid cells have negative values of SES_{FD} when considering all breeding and resident species (Figure 2.2b). Since the sign of

SES_{FD} is partly dependent on how the regional pool is defined, we focus our reporting and discussion on spatial variation in the distribution of SES_{FD} rather than its sign. Areas of relatively high SES_{FD} include India, eastern China and the southern tip of Africa. Most of the Malay Archipelago, Australasia and central Asia have particularly low values of SES_{FD}. The pattern of SES_{FD} for resident species only (where the regional pool is also restricted to residents) shows some similar patterns (Figure 2.2c), but the majority (61.0%) of cells have higher SES_{FD} than when migratory species are included (red areas in Figure 2.2d) and this is particularly evident across the Afrotropics. A majority of continental interior higher-latitude Palaearctic areas have lower SES_{FD} for residents than for all breeding species. Broadly similar results are achieved when all Old World species are included in the regional pool (see Supplementary Figure 3 in Appendix S4: Analyses of species richness and functional diversity using an Old World regional pool).

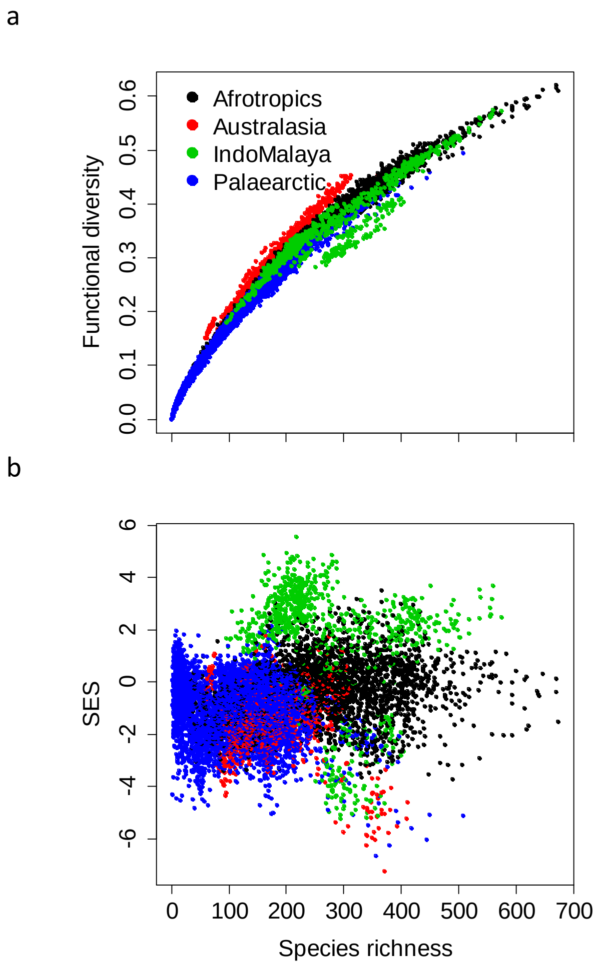

Figure 2.1: The relationship between avian species richness and (a) functional diversity (FD_{obs}) calculated with traits related to resource use (Regression with S and S^2, $r^2 = 0.980$) and (b) Standardised Effect Size of functional diversity (SES_{FD}) calculated using a null model to take account of species richness (Pearson's correlation coefficient = 0.219) for 9,856 1-degree grid cells across the Old World.

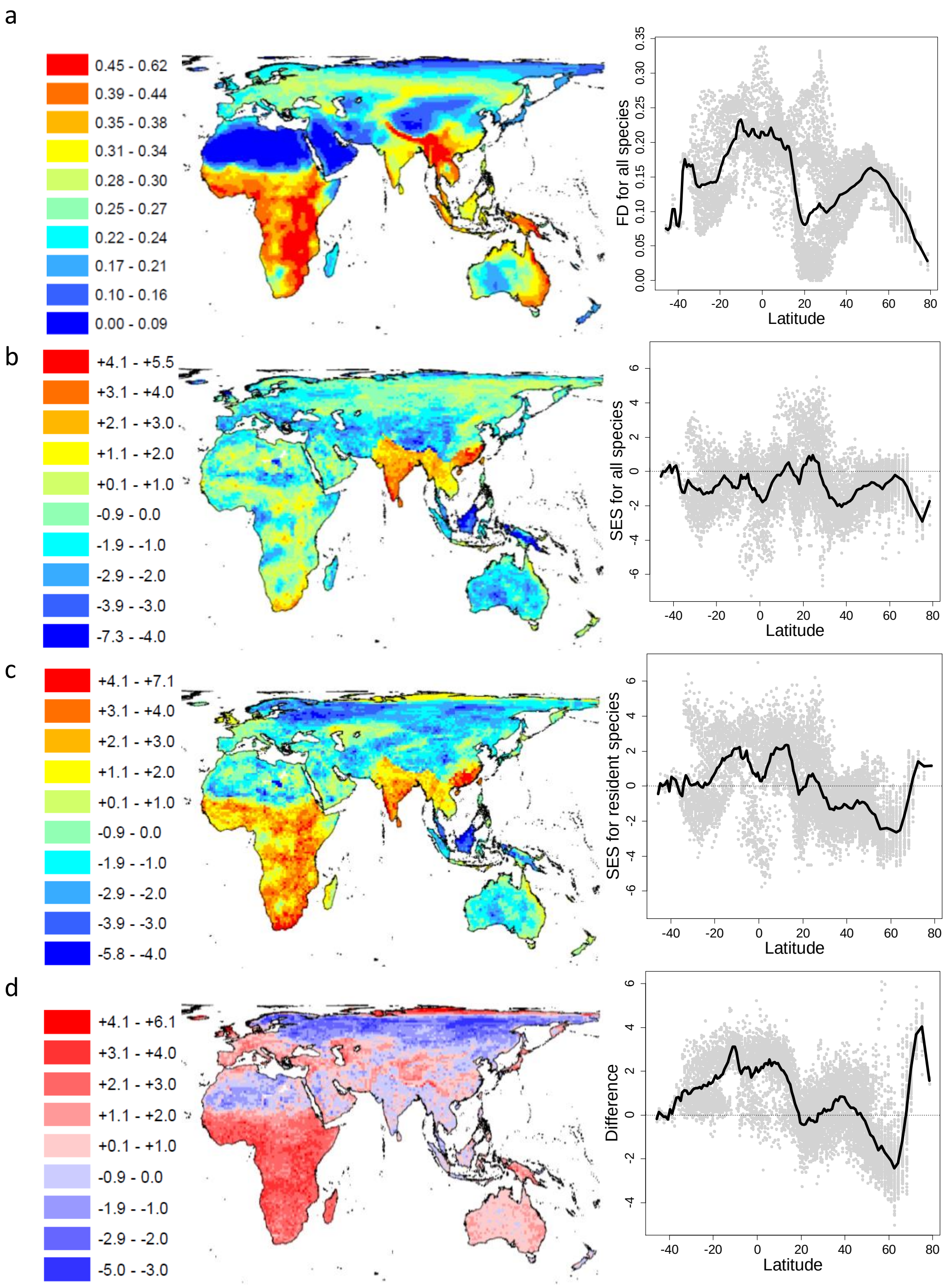

Figure 2.2: (a) The distribution of functional diversity for 9,856 Old World bird assemblages at 1-degree grid cell resolution. (b-c) The distribution of the Standardised Effect Size of Functional Diversity (SES_{FD}) for (b) all breeding birds (5,191 species) and (c) residents (4,826 species). SES_{FD} is the difference between FD_{obs} and FD_{exp} divided by the standard deviation of the FD_{exp} values; high values indicate trait dispersion and low values indicate trait clustering. (d) The difference between SES_{FD} of residents and all breeding species. Red areas are where SES_{FD} is higher for resident species than for all breeding species. Plots show the latitudinal trends: grey points are individual grid cell values and black lines are latitudinal mean values.

The best supported (lowest AIC) univariate models for FD_{obs} for all breeding species were mean annual NDVI, followed by total annual precipitation and then the quadratic model for mean temperature (Table 2.3). Univariate models fitting contemporary climatic factors (the quadratic model for temperature, NDVI and precipitation) were also the best supported for species richness (see Appendix S4: Analyses of species richness and functional diversity using an Old World regional pool). The best supported univariate models for SES_{FD} were for biogeographic realm for both all species and residents only. Of the measured variables, the best supported univariate models for SES_{FD} of all breeding species were the quadratic model for temperature, followed by the same for temperature seasonality and median time since arrival of humans. For resident species only, the best supported models were for temperature seasonality, followed by median time since arrival of humans and the quadratic model for temperature. Therefore, temperature and its seasonality, as well as time since human arrival, seem to be important independent predictors of SES_{FD}.

The final multivariate model for FD_{obs}, which explained 92.3% of the variance in the data, indicated that contemporary climatic variables were important predictors of functional diversity (Table 2.4, Figure 2.3a). In terms of HP components, precipitation was the most important predictor, closely followed by NDVI and temperature seasonality with mean annual temperature in fourth place. Precipitation and NDVI were positively associated with FD_{obs} while temperature and its seasonality both showed quadratic associations that were also mainly positive (Figure 2.4a,b). Of the anthropogenic predictors tested, contemporary extent of cropland and human population density also showed a positive association with FD_{obs} and moderate HP components. Otherwise, contemporary anthropogenic predictors and both historical climatic and anthropogenic predictors yielded HP components of less than 5% each even though they were maintained in the model. The MAM for species richness (see Appendix S4: Analyses of species richness and functional diversity using an Old World regional pool) found similar associations for major climate and anthropogenic predictors except that HP variance associated with temperature seasonality was noticeably less than for FD.

Table 2.3: Single-predictor models of functional diversity (FD_{obs}) calculated with traits related to resource use for all breeding species and Standardised Effect Size of functional diversity (SES_{FD}) calculated using a null model to take account of species richness for all breeding species and residents only. All models also include land area. Models either include just a linear term (L) or a linear and a quadratic term (L and Q). The r^2 is determined by hierarchical partitioning. Significance values: ** <0.0001, *** <0.001, ** <0.01, * <0.05, NS Non-significant. [a] Zero by default, i.e. intercept.**

			FD_{obs} – All breeding species			SES_{FD} - All breeding species			SES_{FD} - Residents only		
	Variable	**Terms**	**AIC (rank)**	**r^2**	**Parameter (±SE)**	**AIC (rank)**	**r^2**	**Parameter (±SE)**	**AIC (rank)**	**r^2**	**Parameter (±SE)**
Contemporary	**Mean annual temperature**	**L**	-55369 (3)	0.59	+0.0273 (±0.0020)****	19139 (2)	0.48	+0.16 (±0.08)*	20260 (4)	0.37	+0.23 (±0.08)**
		Q			-0.0285 (±0.0015)****			+0.42 (±0.06)****			+0.23 (±0.07)***
	Total annual precipitation	**L**	-55397 (2)	0.68	+0.0176 (±0.0009)****	19264 (8)	0.09	+0.17 (±0.03)****	20314 (9)	0.03	+0.07 (±0.04) NS
	Mean annual NDVI	**L**	-55599 (1)	0.66	+0.0164 (±0.0007)****	19254 (6)	0.08	+0.16 (±0.03)****	20317 (10=)	0.00	-0.02 (±0.03) NS
	Temperature seasonality	**L**	-55214 (7)	0.85	-0.0805 (±0.0055)****	19216 (3)	0.27	-1.08 (±0.16)****	20204 (2)	0.68	-0.87 (±0.08)****
		Q			+0.0584 (±0.0040)****			+1.18 (±0.14)****			
	Precipitation seasonality	**L**	-54999 (15)	0.02	-0.0018 (±0.0010) NS	19250 (5)	0.13	+0.46 (±0.10)****	20318 (13=)	0.00	+0.01 (±0.04) NS
		Q						-0.26 (±0.09)**			
	NDVI seasonality	**L**	-55138 (10)	0.25	+0.0070 (±0.0006)****	19279 (13)	0.02	+0.07 (±0.03)**	20302 (6)	0.04	-0.11 (±0.03)****
	Habitat heterogeneity	**L**	-55336 (4)	0.23	+0.0056 (±0.0003)****	19273 (11)	0.01	-0.05 (±0.01)***	20312 (8)	0.00	-0.03 (±0.01)*
	Human population density in 2000AD	**L**	-55160 (9)	0.17	+0.0046 (±0.0004)****	19285 (15)	0.01	+0.02 (±0.02) NS	20317 (10=)	0.01	+0.02 (±0.02) NS
	Cropland extent in 2000AD	**L**	-55189 (8)	0.24	+0.0057 (±0.0004)****	19281 (14)	0.00	-0.04 (±0.02)*	20318 (13=)	0.00	+0.00 (±0.02) NS
	Pastureland extent in 2000AD	**L**	-55043 (14)	0.10	+0.0033 (±0.0005)****	19268 (10)	0.02	-0.09 (±0.02)****	20318 (13=)	0.00	-0.01 (±0.02) NS
Historical	**Temperature change velocity since LGM**	**L**	-55244 (6)	0.21	-0.0054 (±0.0003)****	19263 (7)	0.02	+0.07 (±0.02)****	20308 (7)	0.01	+0.05 (±0.02)**
	Precipitation change velocity since LGM	**L**	-55135 (11)	0.12	-0.0038 (±0.0003)****	19286 (16)	0.00	+0.01 (±0.01) NS	20318 (13=)	0.00	+0.00 (±0.01) NS
	Median arrival time of humans	**L**	-54909 (16)	0.10	+0.0035 (±0.0007)****	19245 (4)	0.02	+0.06 (±0.03)*	20227 (3)	0.09	-0.21 (±0.03)****
	Period since conversion to cropland	**L**	-55072 (12)	0.08	+0.0029 (±0.0003)****	19265 (9)	0.03	+0.04 (±0.05) NS	20317 (10=)	0.00	-0.02 (±0.02) NS
		Q						-0.13 (±0.05)*			
	Period since conversion to pastureland	**L**	-55044 (13)	0.07	+0.0032 (±0.0005)****	19274 (12)	0.03	+0.13 (±0.05)**	20290 (5)	0.06	-0.08 (±0.05) NS
		Q						-0.21 (±0.06)***			-0.22 (±0.06)***
	Biogeographic realm	**AF**	-55325 (5)	0.80	0[a]	17669 (1)	0.83	0[a]	19369 (1)	0.77	0[a]
		AU			+0.0650 (±0.0115)****			-0.05 (±0.19) NS			-1.52 (±0.21)****
		IM			+0.0231 (±0.0035)****			+3.77 (±0.13)****			+1.05 (±0.15)****
		PA			-0.0169 (±0.0023)****			-0.46 (±0.09)****			-1.87 (±0.10)****

Table 2.4: Summary of minimum adequate models (MAMs) for predictors of functional diversity (FD_{obs}) calculated with traits related to resource use for all breeding species and Standardised Effect Size of functional diversity (SES_{FD}) calculated using a null model to take account of species richness for all breeding species and residents only. Significance values: **<0.0001, ***<0.001, **<0.01, *<0.05, NS Non-significant. ^{a} Zero by default, i.e. intercept.**

		Parameter estimate (±SE)		
	Variable	**FD_{obs}** **All breeding species**	**SES_{FD}** **All breeding species**	**SES_{FD}** **Residents only**
Contemporary	**Mean temperature**	+0.031 (±0.002)****	+0.05 (±0.08) NS	-0.16 (±0.09) NS
	Mean temperature^2	-0.022 (±0.001)****	+0.28 (±0.06)****	+0.22 (±0.07)**
	Total precipitation	+0.008 (±0.001)****	-	
	Mean NDVI	+0.007 (±0.001)****	+0.07 (±0.03)**	-0.07 (±0.03)*
	Temperature seasonality	-0.036 (±0.006)****	-0.07 (±0.17) NS	-0.49 (±0.19)*
	Temperature seasonality^2	+0.038 (±0.004)****	+0.58 (±0.14)****	-0.26 (±0.16) NS
	Precipitation seasonality	+0.006 (±0.002)*	+0.41 (±0.09)****	+0.09 (±0.10) NS
	Precipitation seasonality^2	-0.005 (±0.002)**	-0.28 (±0.08)***	-0.15 (±0.09) NS
	NDVI seasonality	+0.001 (±0.001)*	+0.06 (±0.06)*	-0.08 (±0.03)**
	Habitat heterogeneity	+0.003 (±0.000)****	-0.03 (±0.01)*	-
	Human population density in 2000AD	+0.002 (±0.000)****	-	-
	Cropland extent in 2000AD	+0.003 (±0.000)****	-	-
	Pastureland extent in 2000AD	+0.002 (±0.000)**	-0.05 (±0.02)*	-
Historical	**Temperature change velocity since LGM**	-0.004 (±0.000)****	+0.03 (±0.02)*	+0.05 (±0.02)*
	Precipitation change velocity since LGM	-0.002 (±0.000)****	-	
	Median arrival time of humans	-	+0.05 (±0.03) NS	-0.25 (±0.03)****
	Period since conversion to cropland	-0.003 (±0.001)**	-0.05 (±0.01)***	-
	Period since conversion to cropland^2	+0.003 (±0.001)**	-	-
	Period since conversion to pastureland	+0.002 (±0.000)****	+0.14 (±0.05)**	+0.01 (±0.05) NS
	Period since conversion to pastureland^2		-0.17 (±0.05)***	-0.14 (±0.06)*
Covariates	**Realm: Afrotropics**	0^a	0^a	0^a
	Realm: Australasia	+0.015 (±0.012) NS	+0.16 (±0.21) NS	-2.39 (±0.23)****
	Realm: Indo-Malaya	+0.017 (±0.003)****	+3.65 (±0.13)****	+1.08 (±0.14)****
	Realm: Palaearctic	-0.015 (±0.002)****	-0.47 (±0.09)****	-1.78 (±0.10)****
	Land area	+0.002 (±0.000)****	-0.01 (±0.01) NS	-0.03 (±0.01)****
	r^2	0.92	0.84	0.88

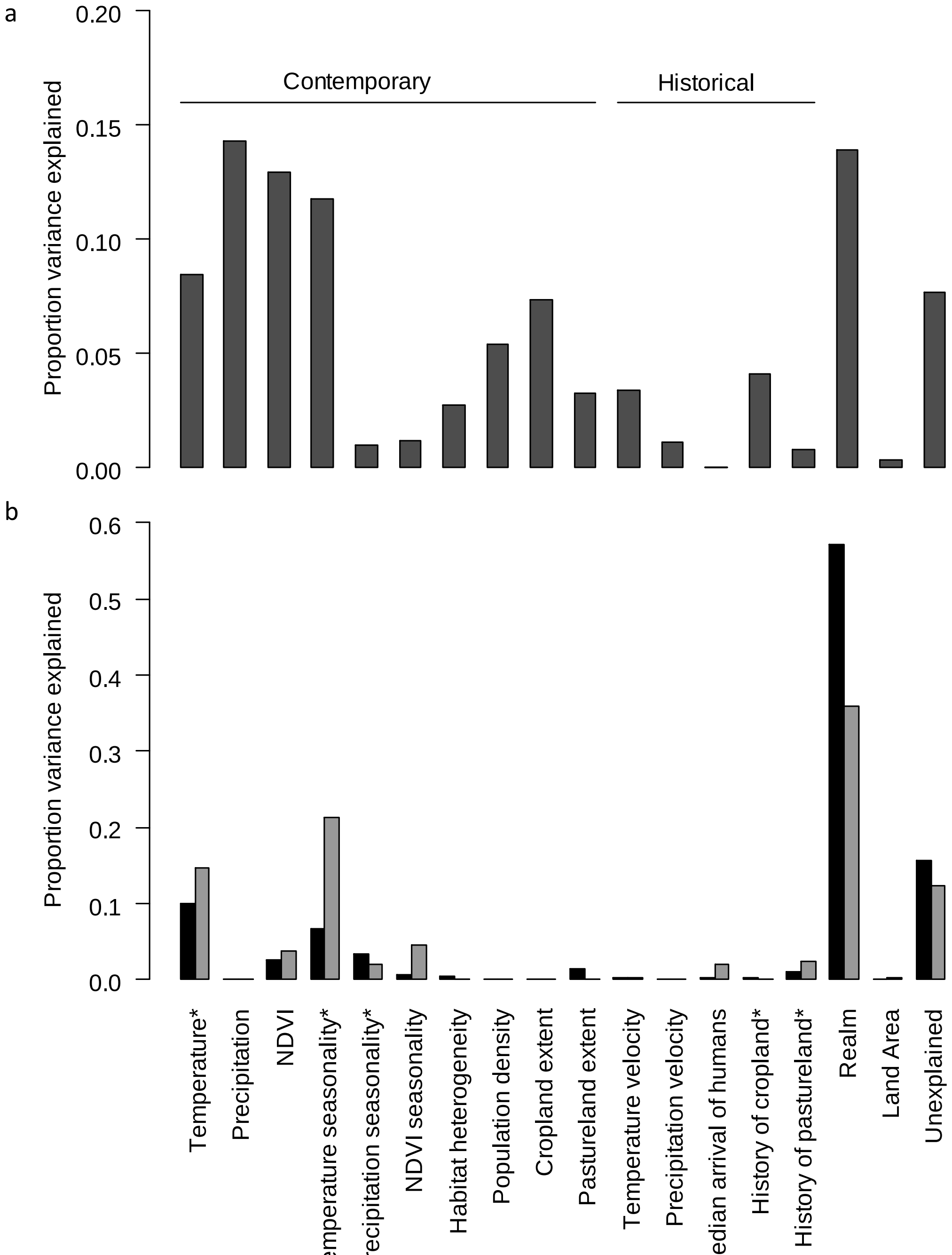

Figure 2.3: The relative importance of predictors as determined by hierarchical partitioning in the minimum adequate spatial (SAR$_{err}$) models for (a) functional diversity (FD$_{obs}$) calculated with traits related to resource use and (b) Standardised Effect Size of functional diversity (SES$_{FD}$) calculated using a null model to take account of species richness for all breeding species and residents only for all breeding birds (black bars) and resident birds (grey bars). Variables marked with an asterisk also include the square term.

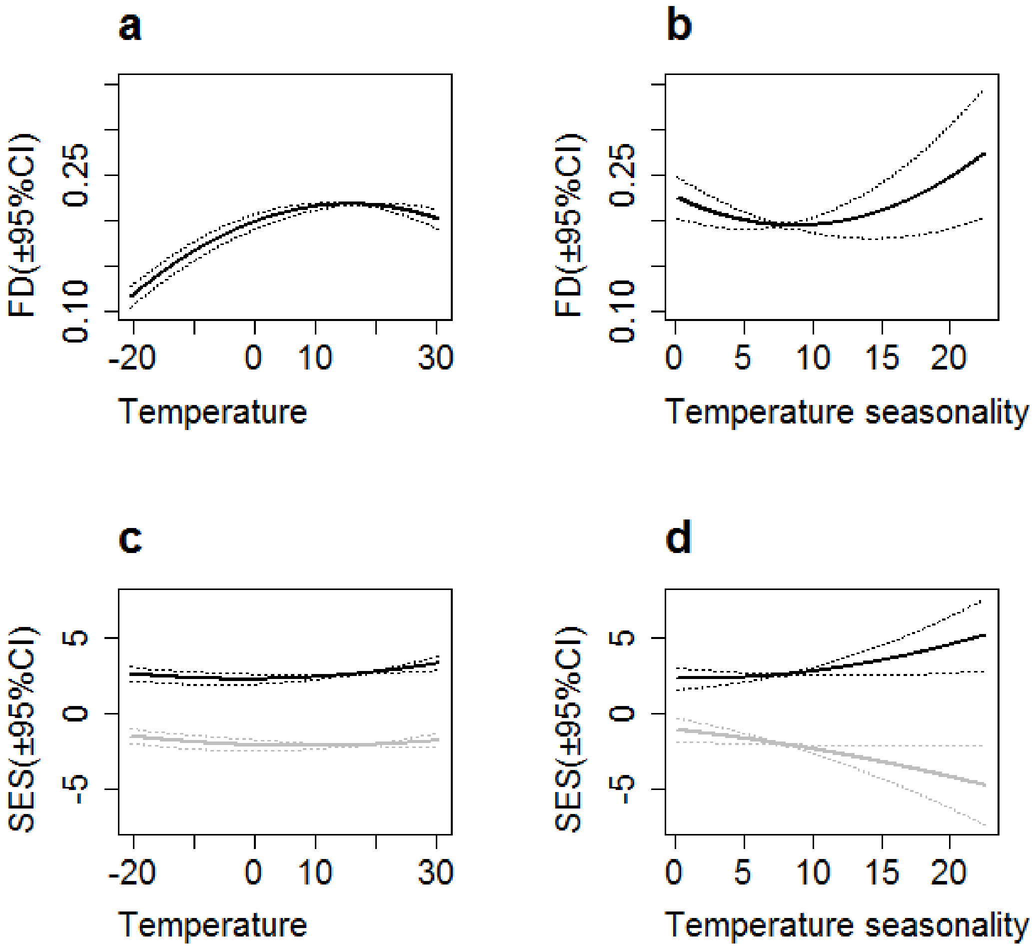

Figure 2.4: Model predictions of (a-b) functional diversity (FD_{obs}) calculated with traits related to resource use and (c-d) Standardised Effect Size of functional diversity (SES_{FD}) calculated using a null model to take account of species richness for grid cells from minimum adequate spatial (SAR_{err}) models for all breeding birds (black lines) and resident birds (grey lines). Predictions are shown for: (a,c) mean annual temperature (°C) and (b,d) temperature seasonality (standard deviation). The predictions for each variable are made whilst holding the other variables fixed at their means across the Old World.

The final multivariate models for SES_{FD}, which explained 84.4% of the variance for all breeding species and 87.6% of the variance for resident species only, indicated that mean temperature and its seasonality were the most important predictors of SES_{FD} (Table 2.4, Figure 2.3b). Mean temperature showed a quadratic relationship with SES_{FD}, being more positively associated with all breeding species than with residents only but showing greater HP variance explained for residents (Figure 2.4c). Temperature seasonality showed a quadratic relationship with SES_{FD} that was positive for all breeding species (explaining 6.7% of the variance), but negative for residents only (explaining 21.4% of the variance) (Figure 2.4d). Compared with the model for FD_{obs}, anthropogenic predictors showed relatively little power in explaining either SES_{FD} for either all breeding species or residents. Overall, contemporary predictors explained 25.3% of the variance in SES_{FD} for all breeding species and 46.5% for resident species. Historical predictors explained 2.0% of the variance in SES_{FD} for all breeding species and 4.7% for resident species.

2.5 Discussion

At macroecological scales avian FD shows no evidence of approaching a saturating relationship with species richness indicating low levels of functional redundancy (Figure 2.1a). There is a quadratic relationship with species richness, which explains 98% of the variance, indicating FD is very largely a function of species numbers. Nevertheless, the variation around this relationship is important if we consider that grid cells containing 300 bird species may represent FD of as low as 0.3 in parts of Indo-Malaya or as high as 0.45, a 50% increase, in parts of Australasia.

Comparison of large-scale variation in SES_{FD} for all breeding species and for residents (Figure 2.2b,c) reveals important insights concerning the contribution of migrants to assemblages at different latitudes. The contribution of migrants to breeding assemblages shows increases in SES_{FD} at higher northern latitudes compared with SES_{FD} for residents only, reflecting apparent increases in average niche breadth. In contrast the low resident species richness of northern Palearctic areas appears to represent a relatively filtered subset that is functionally constrained, presumably by the eco-physiological demands of year-round survival in a seasonally challenging environment. At low latitudes, residents are relatively functionally over-dispersed with wider niche breadths compared with higher latitudes. The contribution of migrants has the effect of lowering SES_{FD} through overall increases in niche packing at low latitudes, at least within the Afrotropics.

Both univariate regression and MAM results support the observed patterns. As with numerous macroecological analyses of latitudinal gradients in species richness (e.g. Hawkins *et al.*, 2003a), this study finds strongest support for the productive energy hypothesis in explaining FD distribution across the Old World. This is consistent with previous analyses of latitudinal gradients of single traits and functional guilds. Nevertheless, our MAM for FD has a higher HP variance component associated with precipitation than our species richness MAM, while that for NDVI is of similar magnitude (Figure 2.3a and Appendix S4: Analyses of species richness and functional diversity using an Old World regional pool).

Mean temperature is also known to be strongly associated with large-scale variation in species richness of major vertebrate taxa (e.g. Davies *et al.*, 2007a), with species richness of particular guilds such as avian herbivores and scavengers (Kissling *et al.*, 2012) and with individual traits associated with physiological tolerances e.g. body size (Olson *et al.*, 2009). In the present study, temperature seasonality has greater explanatory power than mean temperature for FD but somewhat lower explanatory power for species richness. This increase in the relative importance of temperature seasonality from species richness to FD is complemented in the results for SES_{FD}. Temperature seasonality is more explanatory than productivity measures (either annual mean or seasonality) for SES_{FD} of all breeding species and much more explanatory for SES_{FD} of residents (Figure 2.3b). Areas of low seasonality, hence more predictable resources, may permit greater specialisation and species packing (Stevens, 1989; Pianka, 1966) meaning that traits are relatively under-dispersed. For example, the niche width of vertebrates is positively associated with the temperature and precipitation seasonality within their resident localities (Quintero & Wiens, 2012) and tropical bird assemblages have more specialised diet and habitat niches (Belmaker *et al.*, 2012).

Interestingly, the slope of relationship of temperature seasonality switches from positive for SES_{FD} of all breeding species to negative for SES_{FD} of residents (Figure 2.4d). These results confirm that at high northern latitudes summer breeding assemblages are relatively unaffected by seasonality, hence more functionally diverse, while year-round residents are more functionally constrained by seasonal challenges and the species pool is limited to the least specialized species, which favours niche overlap. Species that migrate can track a more similar climate through the year by moving to higher or lower latitudes or altitudes. The importance of seasonality in these analyses is consistent with the suggestion of Safi *et al.* (2011) that the latitudinal gradient of mammal functional diversity could be partly attributed to temperature seasonality effects.

The measured historical variables that remain in the MAM for SES_{FD} explain a very small proportion of the variance. However, biogeographic realm explained by far the greatest proportion of variance in SES_{FD} for all breeding species as well as resident species (Figure

2.3b). This factor is thought to represent important differences in the histories of each region (Buckley & Jetz, 2007). Therefore, its importance in our analyses suggests that there are historical processes whose influences are not explicitly captured in the predictors we found to be associated with SES_{FD}, such as historical dispersal, isolation, diversification and extinction (Schuldt & Assmann, 2009). It may also indicate that there are other important contemporary environmental variables that have not been included in our models. The relatively low proportion of variance explained by anthropogenic factors (both contemporary and historical) for FD and especially SES_{FD} may in part be explained by the use of Extent of Occurrence (EOO) maps for species' distribution. Due to effects of habitat suitability, species do not occur in all areas within their EOO (Hurlbert & White, 2005). Therefore, the value calculated for functional diversity of areas that have been particularly impacted by human effects may be inflated by the use of EOO range maps. This could bias patterns in SES_{FD} more than FD since species' susceptibilities to anthropogenic impacts are likely to be non-random with respect to traits. Nevertheless, it is notable that at the scale of this analysis that anthropogenic impacts on average niche breadths appears to be slight.

Since FD may affect ecosystem processes (Cadotte *et al.*, 2011), understanding the predictors of its distribution could help us to identify areas that might be most at risk of decreasing delivery of those processes in the face of future environmental change. Climate change is expected to alter migration patterns of birds and is already affecting community composition in Europe (Lemoine *et al.*, 2007). In the present study, SES_{FD} of cells varied depending on whether migratory species were included (Figure 2.2b-d); changes in the distribution of migratory birds will have consequences for the FD of assemblages, particularly where migratory species make up a large proportion of the overall species richness (Somveille *et al.*, 2013). Since functional diversity is thought to affect ecosystem processes (Cadotte *et al.*, 2011; Mason *et al.*, 2005), migratory species might be contributing more effectively than residents alone to certain processes during the breeding season (e.g. migratory insectivores consuming pest species (e.g. Ji *et al.*, 2008)) because of their particular combination of traits. Stronger declines of long-distance migrants related to climate change have been observed in more seasonal forest habitats compared to less seasonal marsh habitats (Both *et al.*, 2010); areas of high seasonality where SES_{FD} is lower for resident species may be particularly negatively affected by the loss of migratory species which increase SES_{FD} in the breeding season.

2.6 Conclusions

Of the predictors tested, biogeographic realm was very important in explaining the large-scale distribution of avian FD, and the most important variable in explaining avian SES_{FD}, across the Old World. Of the continuously measured variables, contemporary climate variables were found to be the most important; productive energy variables were associated with FD, while SES_{FD} was most strongly associated with mean temperature and its seasonality. These results indicate that latitudinal gradients of breeding bird assemblages are underpinned by an increase in average niche breadth with increasing temperature seasonality. However, this belies a pattern of restricted functional diversity amongst resident assemblages at high latitudes. Nevertheless, the finding that biogeographic realm explained more variance than any of the continuous variables, suggests that there are unmeasured historical or contemporary processes that influence the distribution SES_{FD}. By considering the SES_{FD} of resident species separately, it has been demonstrated that the relationships with variables tested and their relative importance is different to when migratory species are included. Therefore, future changes in the distribution and abundance of migratory species as a result of climate change could have profound effects on the functional diversity of bird communities in some regions.

Chapter Three: Functional trait space use by birds at the macroecological scale

3.1 Abstract

Aim: In this chapter, we investigate the environmental correlates of the distribution of the occupancy of functional trait space by breeding birds across the Old World at the macroecological scale in order to provide new insights into the relative importance of different hypotheses of latitudinal diversity gradients.

Location: The Old World (Palaearctic, Indo-Malaya, Afrotropics and Australasia).

Methods: Species were arranged in multidimensional functional trait space and multivariate methods – volume of convex hull (functional richness) and principal coordinates analysis (PCoA) – were used to investigate and compare the occupancy of this space by all breeding and resident species, and residents only, in approximately 1-degree cells across the Old World. Simultaneous autoregressive models and hierarchical partitioning were used to identify the most important predictors of (i) the large-scale distribution of functional richness, and (ii) the range (maximum minus minimum) and mean scores for each of the four most important PCoA dimensions.

Results: Functional richness varied between 0 and 0.31. Cells with high functional richness (>0.28) were mainly found in tropical regions and areas of high elevational range, whilst cells with the lowest functional richness (<0.17) were found in arid and Polar Regions. There were signficiant differences in the functional richness between biogeographic realms; FRic was highest in Australasia and lowest in the Palaearctic, with biogeographic realm explaining 11.5% of the variance for all breeding species and 19.7% for residents. Contemporary environmental variables were important in explaining the distribution of functional richness, particularly positive associations with precipitation and temperature; precipitation explained 24.1% of the variance in FRic for all breeding species and 13.3% for residents.

Precipitation also showed positive relationships with the range of habitat strata used (PCoA dimension one) and the trophic range of assemblages (PCoA dimension three). High precipitation was associated with higher habitat strata and higher trophic levels. In regions of high temperature seasonality, resident assemblages showed a restricted range of aquatic-terrestrial niches (PCoA dimension two) and were less likely to use aquatic habitats for foraging. Regions of low temperature were associated with greater body mass (PCoA dimension four).

Main conclusions: The distribution of functional richness of bird assemblages across the Old World is best predicted by contemporary environmental variables, in particular supporting the role of productive energy in latitudinal diversity gradients. There was also evidence for ecological filtering associated with harsh environmental conditions, with low functional richness in very cold and/or dry regions. Consideration of each of the main trait dimensions separately indicated the importance of both productive and ambient energy, as well as environmental stability (temperature seasonality), but there was little support for the role of habitat heterogeneity or historical variables.

Keywords: Environmental filtering, functional richness, functional traits, Old World, principal coordinates analysis, redundancy, productive energy, ambient energy, environmental stability, habitat heterogeneity, historical biogeography

3.2 Introduction

Latitudinal gradients have been described for a wide range of ecological phenomena including species richness (e.g.Blackburn & Gaston, 1996; Davies *et al.*, 2007a), body size (e.g. Olson *et al.*, 2009) and geographic range size (e.g. Stevens, 1989; Orme *et al.*, 2006). They have been attributed to a variety of causes including contemporary environment (e.g. Currie & Paquin, 1987; Francis & Currie, 2003) and historical biogeography (e.g. Ricklefs, 1987; Mittelbach *et al.*, 2007), with environmental energy being among the best supported explanations (e.g. Wright, 1983; Currie, 1991) along with habitat heterogeneity (e.g. Kerr *et al.*, 2001; Rahbek & Graves, 2001; Davies *et al.*, 2007a). Both of these explanations require consideration of species' niches and traits: some species may be absent from particular regions because they do not have traits that allow survival in the local environmental conditions, e.g. small-bodied birds are less well adapted to the physiological demands of cold temperatures during the winter at high latitudes (ambient energy hypothesis, e.g. Bellocq & Gomez-Insausti, 2005; Olson *et al.*, 2009); more species may occur in high energy areas such as the tropics because abundant resources allow coexistence of species with narrower niches and therefore more similar traits (productive energy hypothesis, e.g. Tognelli & Kelt, 2004); or areas with a greater variety of habitats (both in terms of landuse and topography) allow greater spatial turnover of species because of adaptations to different habitats (habitat heterogeneity hypothesis, e.g. Kerr *et al.*, 2001).

As well as the importance of mean annual energy in species-energy relationships, authors have highlighted the role of energy seasonality (Carrara & Vázquez, 2010). High species richness might be evidence of finer niche partitioning (Hutchinson, 1959); areas of high environmental stability (which may also be areas of high productive energy) can support populations of species that specialise on a narrow range of resources. Since seasonality is lower (and productive energy higher) in the tropics, an extension of this hypothesis is that niches are narrower at lower latitudes. Diet and habitat specialisation has been found to be higher in the tropics for bird assemblages (Belmaker *et al.*, 2012) and evidence supports the niche breadth hypothesis for the distribution of British birds (Evans *et al.*, 2006). This pattern has also been found in other taxa: for example habitat and dietary niche breath increases with latitude for African primates (Eeley & Foley, 1999) and fleas (Krasnov *et al.*, 2008), although there are also many counterexamples to this hypothesis (Vázquez & Stevens, 2004). The latitude-niche breadth hypothesis is related to Rapoport's rule that purports a positive correlation between a species' geographical range size and its latitude (Stevens, 1989). The underlying assumption of this rule is that there is a selection pressure for species at higher latitudes to have wider climatic tolerances since the climate is more fluctuating (Janzen, 1967). The global distribution of bird range sizes does not conform to Rapoport's rule, however range size is significantly (albeit weakly) negatively correlated to species richness (Orme *et al.*, 2006). The majority of bird species that breed in high latitudes avoid large climate fluctuations by migrating to lower latitudes post-breeding (Berthold, 1993). Therefore, within-year seasonality of energy and resources may show a stronger signal than among year variation for resident species richness particularly (Carrara & Vázquez, 2010).

As well as contemporary drivers of diversity, many authors have suggested that historical processes may be at least equally important; the differences in diversity between ecosystem types in different locations that have experienced different evolutionary histories but similar contemporary climatic conditions are purported to be evidence that current environmental conditions cannot explain all the variation in diversity (e.g. Latham & Ricklefs, 1993; Ricklefs *et al.*, 1999; Ricklefs, 2004). Others argue that diversity is primarily regulated by current environmental conditions; historical effects are transitory and the signal has been lost as a result of species' responses to contemporary predictors (e.g. Currie & Paquin, 1987; Francis & Currie, 1998; Whittaker & Field, 2000). Lack of empirical support for a historical signature could in part be due to a lack of high resolution quantitative data for past climate conditions (Araújo *et al.*, 2008). It has been suggested that historical explanations of biodiversity distribution might not be testable (Francis & Currie, 1998), but with increasing availability of suitable data at an appropriate resolution historical explanations of current macroecological distribution of biodiversity deserve greater attention (Beck *et al.*, 2012). Indeed, understanding how species have responded to past processes may help us to understand how they will respond to future environmental change (Kerr & Dobrowski, 2013).

Analysis of the global distribution of body size in birds revealed that small-bodied birds were over-represented in species rich regions and therefore that species richness may be partly explained by limits to the trait composition of assemblages (Olson *et al.*, 2009). Therefore, consideration of more traits other than body size may provide further insight into the causes of diversity gradients and yield greater understanding of the relative importance of mean energy, seasonality, habitat heterogeneity, historical processes and other suggested drivers of diversity.

The division of resources between species within a community leads to interspecific competition and the strength of this competition is determined by the similarity of their niches. The niche was described by Hutchinson (1957) as an "*n-dimensional hypervolume*" where each dimension represents an environmental variable. To consider instead the variety of niches represented by species in an assemblage (functional diversity), you can use a t-dimensional volume, where each dimension represents a trait (Villéger *et al.*, 2008). The arrangement of species in this multidimensional functional trait space provides information on the overall volume of niche space occupied (functional richness; Mason *et al.*, 2005), the use of this space by the constituent species and the importance of particular traits in differentiating between species (Pease *et al.*, 2012; Inward *et al.*, 2011). Consideration of the use of functional trait space by assemblages can inform our functional ecological understanding of community assembly (Mouchet *et al.*, 2010), the relationship between biodiversity and ecosystem services (Clark *et al.*, 2012) and community change along spatial environmental gradients (Schirmel *et al.*, 2012; Gerisch *et al.*, 2012).

Functional richness indicates the efficiency of the use of resources available to assemblages, i.e. low functional richness signifies that some potential niches are unoccupied either because species that could make use of particular resources are missing or because environmental conditions mean that the resources themselves are unavailable (Mason *et al.*, 2005). Species that fill those niches may be absent from a particular assemblage because they are not adapted to the local environmental conditions. Thus the volume and use of functional trait space may in part be determined by environmental filtering (Schleuter *et al.*, 2012; Bello *et al.*, 2013). Investigation of traits of coexisting species has shown that environmental filtering is an important explanation of community assembly in a tropical dry forest (Lebrija-Trejos *et al.*, 2010), bird communities in Great Britain (Petchey *et al.*, 2007; Mendez *et al.*, 2012) and roadside plants in England (Thompson *et al.*, 2009). Low functional richness might therefore be expected to be associated with more extreme environmental conditions such as very low temperatures or precipitation.

In this chapter, birds are used as a model system to investigate the use of functional trait space. Birds contribute to a number of beneficial ecosystem processes, e.g. seed dispersal, pollination, pest control, waste disposal such as scavenging carcasses, nutrient deposition and ecosystem engineering such as nest-hole creation (Şekercioğlu, 2006). If there is high functional redundancy (i.e. a saturating relationship between increasing species richness and functional diversity), then the processes within that community may be resilient to some species loss (Naeem, 1998) as has been projected for plant community change in eastern Australian rainforests resulting from climate change. Hence, redundancy of trait combinations may act as a buffer protecting ecosystem function (Gallagher *et al.*, 2013). Alternatively, functional diversity of bird communities in Great Britain indicates that there is little redundancy (Petchey *et al.*, 2007), which suggests that extinctions in this area could have serious consequences.

The majority of bird species that breed in high latitudes migrate (Berthold, 1993) and those species that migrate tend to exploit food resources that are not available in their breeding grounds year-round (Newton, 2008). Therefore, the functional richness of resident species in highly seasonal areas could be expected to be lower than when migratory species are included, and their position in functional trait space is likely to reflect the availability of resources during the winter months. Separate consideration of all breeding species and resident species only may therefore reveal different patterns of occupancy of functional trait space and different environmental predictors of those patterns.

In this chapter, we use a multivariate trait space approach to further understand the latitudinal gradients of diversity of bird assemblages across the Old World. We investigate the total volume of trait space – functional richness (Villéger *et al.*, 2008) – and its main dimensions in order to identify the importance of environmental constraints on particular aspects of species' ecologies. We compare patterns of functional richness and trait space occupancy for all species present in the breeding season and only resident species since this may reveal alternative explanations for species that do not migrate away from areas of high seasonal fluctuation.

3.3 Methods

3.2.1 Distribution of bird species

Analyses of distributions were carried out using ArcMap 9.3 (ESRI, 2010). Shape files of bird species ranges were provided by BirdLife International (Birdlife International & Natureserve, 2011). These maps are the most complete and accurate current estimates of Extent of Occurrence maps for all extant bird species and have been produced using known locations (e.g. geo-referenced point locality records, collecting locality of museum specimens) and expert opinion (see Buchanan *et al.* (2011) for details). For each species, the areas in which it is considered extant or probably extant through the year or the breeding season were included. Areas where a species was considered possibly extant or possibly extinct or where its presence was uncertain were excluded. 58 seabirds, defined as those species which predominately feed at sea and are described as pelagic or feeding offshore (Del Hoyo *et al.*, 1992; 1996), were excluded from the analysis. These exclusion criteria were consistent with those used in other macroecological analyses of bird distributions (e.g. Orme *et al.*, 2006; Hurlbert & Jetz, 2007).

The range maps of bird species presence in the Palaearctic, Afrotropical, Indo-Malayan and Australasian realms (Olson *et al.*, 2001) were sampled to a Behrmann cylindrical equal-area projection with 96.486 km x 96.486 km grid cell resolution, approximately equivalent to 1°. Exclusion of grid cells with less than 50% land-area resulted in 9,856 cells across the four realms. Species were scored as present in a grid cell when there was any amount of range map overlap. The regional species pool for all species contained 5,191 species and in each grid cell species richness (calculated by summing the species presence in each cell) ranged from 1 to 674 (median = 169). The regional species pool for resident birds contained 4,826 species and species richness ranged from 1 to 672 (median = 79).

3.2.2 Functional traits

We used traits selected for their role in resource use for our investigations into avian assemblage occupancy of ecomorphological trait space (Table 2.1). Feeding location, strata used and diet were treated as binary traits since the categories are not exclusive. For example, a bird could feed both on the ground and in vegetation. Trait values for each species were collated using a variety of sources (Appendix S1: Sources used for bird trait data). Where data were not available for individual species (<10% of species/trait combinations), genus, or failing that family, values were used (Table 2.1). 14.5% of species were assigned values for one trait using the genus average and 15.3% of species were assigned values for more than one trait using the genus average. 3.1% of species were assigned values for one trait using the family average and 1.1% of species were assigned values for more than one trait using the family average. Overall, 90.7% of the species/trait combinations used were specific to individual species, 8.4% were genus averages and 0.9% were family averages.

Principal Coordinates Analysis (PCoA), also known as multidimensional scaling (Gower, 1966), was used to describe the distribution of species within the overall functional trait space defined by all species within our Old World dataset. PCoA is similar to Principal Components Analysis (PCA), but can be used for traits which are not measured on a continuous scale. The PCoA is used to ordinate species along axes representing variation in associated sets of traits so that the distances between species are approximately equal to the dissimilarities in their trait values. The trait vectors and factors were fitted to the PCoA to identify which functional traits are most important in differentiating between species in terms of their functional ecology. Derived from this PCoA, functional richness *sensu* Villéger *et al.* (2008) was calculated for each grid cell as the convex hull volume defining the subset of functional space occupied by centroids for all species present. The mean and range of scores for each of the first four PCoA dimensions were calculated for each grid cell to investigate their spatial variation. Range of PCoA dimension scores in each grid cell was logit-transformed prior to analyses since these effectively had the property of proportional response variables.

3.2.3 Model predictors

The model predictors chosen to investigate the distribution of functional trait space use (functional richness and mean/range of PCoA dimension scores) are summarised in Table 2.2. Raw data for each predictor were reprojected and resampled to the same equal-area projection and resolution as the species data. Details on data sources are available in Chapter 2. We included land area of each grid cell as a covariate in all models to control for species-area effects (Macarthur & Wilson, 1967; Preston, 1960; 1962). Biogeographic realm was included as a factor in all models to take account of potentially large biogeographical differences between the four realms in a given response variable that are not accounted for by our environmental predictors. In this context, realm represents a surrogate index of different biogeographic histories. Species richness and species richness^2 were included as covariates in models of functional richness and range of PCoA scores, since both of these measures increase with species richness. Bi-plots of the predictors were inspected and the variance inflation factors (VIF) calculated to identify any collinearity. Since each of the VIF values was <10 (Quinn & Keough, 2002), all predictors in Table 2.2 were considered in model selection. The following variables were log-transformed because they showed right-skew: mean precipitation, temperature change velocity, precipitation change velocity and contemporary population density. Resampling of all environmental and anthropogenic data was carried out in SAS version 9.2.

3.2.4 Accounting for spatial autocorrelation

Analyses of spatial data require special consideration because points that are closer to one another in space are more likely to have similar values (data are spatially autocorrelated) and therefore do not constitute independent samples (Legendre, 1993; Koenig, 1999). Simultaneous autoregressive (SAR) models were used to account for the spatial autocorrelation in the data since these methods have been shown to perform well compared with non-spatial regression methods and with other methods that reduce spatial autocorrelation (Tognelli & Kelt, 2004; Kissling & Carl, 2008; Beale *et al.*, 2010). A spatial error (SAR_{err}) model was used, which accounts for spatial autocorrelation in model residuals by adding a spatially-dependent error term to an OLS regression model. This method was chosen because SAR_{err} effectively reduces spatial autocorrelation, shows good precision in parameter estimates and good type I error control (Kissling & Carl, 2008). A spatial weights matrix was created which scores pairs of cells according to their relative positions and therefore the likelihood that they are auto-correlated; each cell had up to 8 neighbours – i.e. any cells that share a border or vertex. The spatial weights matrix was row standardised so that the sum of each row was equal to one and proportional weights were calculated according to the number of neighbours of each cell (Kissling & Carl, 2008). The spatial weights matrix was used to calculate a variance-covariance matrix to account for patterns attributable to the values of variables in neighbouring cells (Kissling & Carl, 2008). Using these attributes, Moran's I was close to zero at all distances, indicating that the residual autocorrelation was successfully removed. Computation of SAR models was carried out using the *errorsarlm* function in the *spdep* package (Bivand, 2006).

3.2.5 Backwards selection of models and hierarchical partitioning

Single-predictor models of each variable (with land area and biogeographic realm as covariates) were performed to check the strength and direction of individual relationships. Starting with a full model that fitted all predictors (Table 2.2) we used backwards removal (based on improvement of AIC) to arrive at a minimum adequate model (MAM) with the lowest AIC. Forwards stepwise model selection resulted in the same final model. We used hierarchical partitioning to establish the relative importance of the predictors in the MAM.

Since this method cannot be applied directly to SAR models, we first removed the spatial component of the fitted values to create a new response variable. OLS and hierarchical partitioning were performed on this new response variable using the same predictor combinations(Belmaker & Jetz, 2011). Hierarchical partitioning was carried out using the *calc.relimp* function in the *relaimpo* package (Groemping, 2010).

3.4 Results & Discussion

Cells with high functional richness were mainly found in tropical regions and areas of high elevational range, such as the Himalayas (Figure 3.1a,b). Cells with the lowest functional richness were found in Polar Regions and arid areas such as the Sahara desert. Functional richness increased with species richness, but the relationship was saturating (Supplementary Figure 4). With respect to total ecomorphological space occupied by avian assemblages, this suggests some redundancy at high levels of species richness. This is consistent with Cumming & Child (2009), who found that the richness of functional groups based on beak morphology in South African birds increased with species richness, but plateaued at high species richness. However, since classifying species into functional groups necessarily involves some loss of information, the results that we present using a continuous measure of functional diversity provide stronger evidence of ecological redundancy in species rich assemblages.

Contrastingly, Petchey *et al.* (2007) found no redundancy in assemblages of British birds using the FD metric, which is an indirect measure of functional richness and has been found to be highly correlated with FRic (Mouchet *et al.*, 2010). Indeed, comparison of functional richness of assemblages in this study with the FD metric used by Petchey *et al.* (2007) using data from Chapter 2 reveals that the two measures are highly correlated across our dataset (Pearson correlation, r=0.83). However, Petchey *et al.* (2007) found a saturating relationship between species richness and FD in assemblages drawn randomly from the regional pool and the scale of their analysis was much smaller than this study, with a regional pool of 192 species and a maximum species richness of 125 (compared to this study's regional pool of 5,191 species and a maximum species richness of 674 species). Although functional richness describes the volume of trait space occupied, it provides no information about the distribution of species within the convex hull. In other words, its magnitude is dependent on the trait values at the extremes of occupied trait space. However, all species in an assemblage contribute to the FD metric used by Petchey *et al.* (2007), which may explain why the relationship between functional richness and species richness indicates a greater degree of redundancy than FD. The ecological relevance of each of the indications of the degree of redundancy will depend in part on whether species with extreme trait values are more important to ecosystem processes than species closer to the assemblage centroid in trait space.

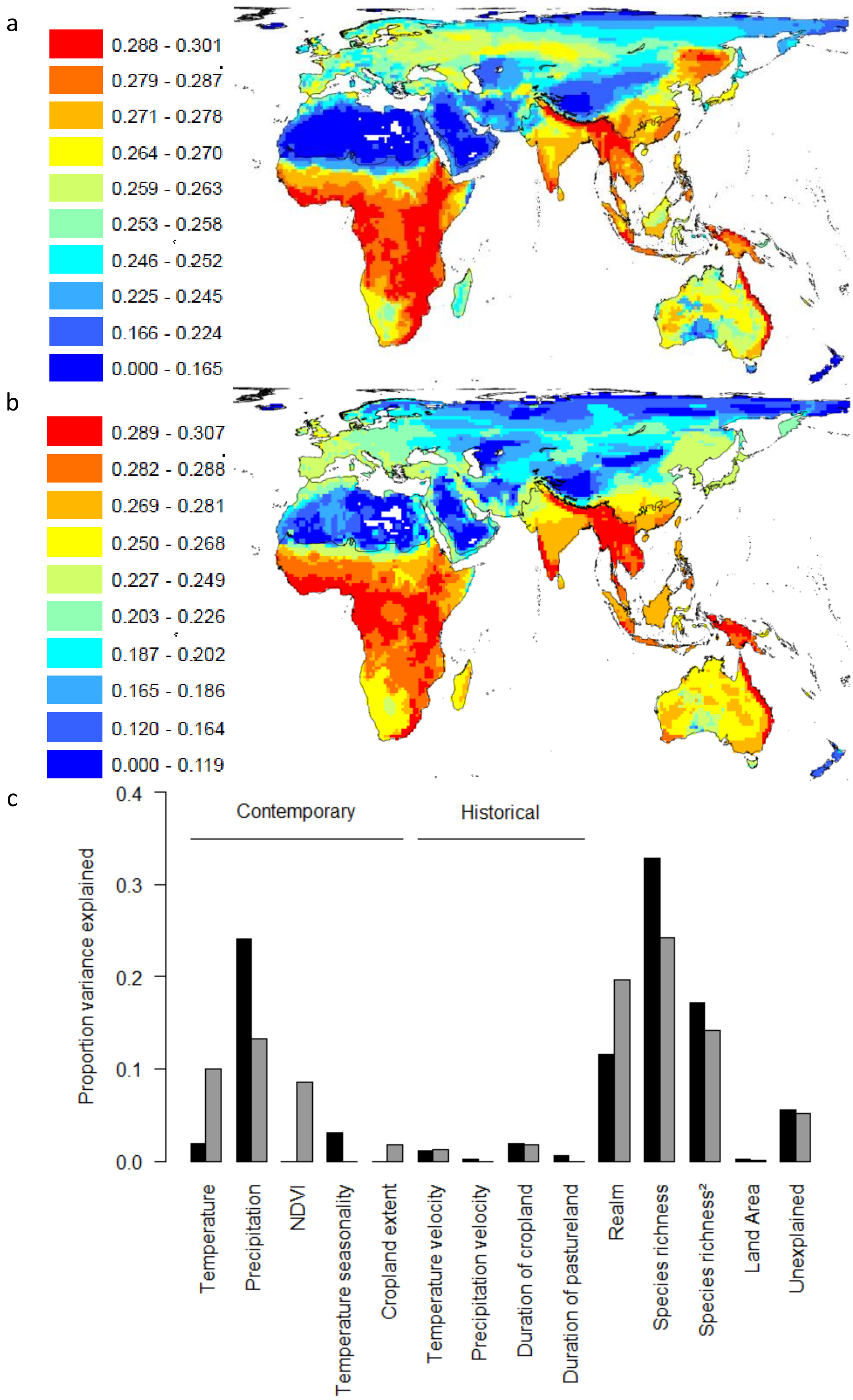

Figure 3.1: The functional richness (volume of trait space occupied) across the Old World of cells of (a) all bird species present during the breeding season and (b) resident species. Data are divided into deciles. (c) The relative importance of predictors as determined by hierarchical partitioning in the final models for functional richness for all birds (black bars) and resident birds (grey bars).

PCoA dimensions one to four explained 31.3%, 15.2%, 14.4% and 8.2% respectively. The later dimensions were not considered because they each explained <7% of the variance and did not show clear and interpretable trait associations. Positive scores of dimension one reflect species' associations with activity in low habitat strata (ground/water to grass/low vegetation) and foraging on the ground, whereas negative scores of dimension one reflect associations with activity in high habitat strata (middle layers to canopy or above), foraging in vegetation and feeding on nectar (Figure 3.2a). Hence the greatest variation among species traits was found to be for habitat strata used and where species forage. Positive scores of dimension two were associated with foraging on or in water and negative scores were associated with activity in grass/low vegetation, shrubs/understorey and the middle layers; therefore this dimension ordinated species according to their positions along a gradient from predominantly aquatic to predominantly terrestrial feeding (Figure 3.2a). Positive scores of dimension three were most strongly associated with foraging in the air and feeding on vertebrates or invertebrates. Negative scores were associated with herbivorous feeding (mainly seeds or nuts, fruit or berries and vegetation or other plant parts); therefore this dimension separated species according to a carnivory-herbivory gradient (Figure 3.2b). Positive scores of dimension four were most strongly associated with body size, followed by feeding on vertebrates and foraging on or in the water. Negative scores were associated with aerial insectivores (Figure 3.2b); therefore this dimension separates species according to body size and prey size. The distribution of the range of values and their mean for each of the dimensions is shown in Figure 3.3.

Since many important traits co-vary with body size it has been suggested that body mass variation is a suitable proxy for FD (Fritz & Purvis, 2010) avoiding the need for very time-consuming macroecological data collation of a number of traits. Body size tends to be one of the more readily available traits; for example, data on the body mass of ~85% of bird species are available in Dunning's (2007) Handbook of Avian Body Masses. However, we found that in the PCoA analysis, body mass did not load strongly onto dimension one which explains most (31.3%) of the variation in the data. In fact, body mass most strongly aligned with dimension four which only explains 8.2% of the variation in the trait data.

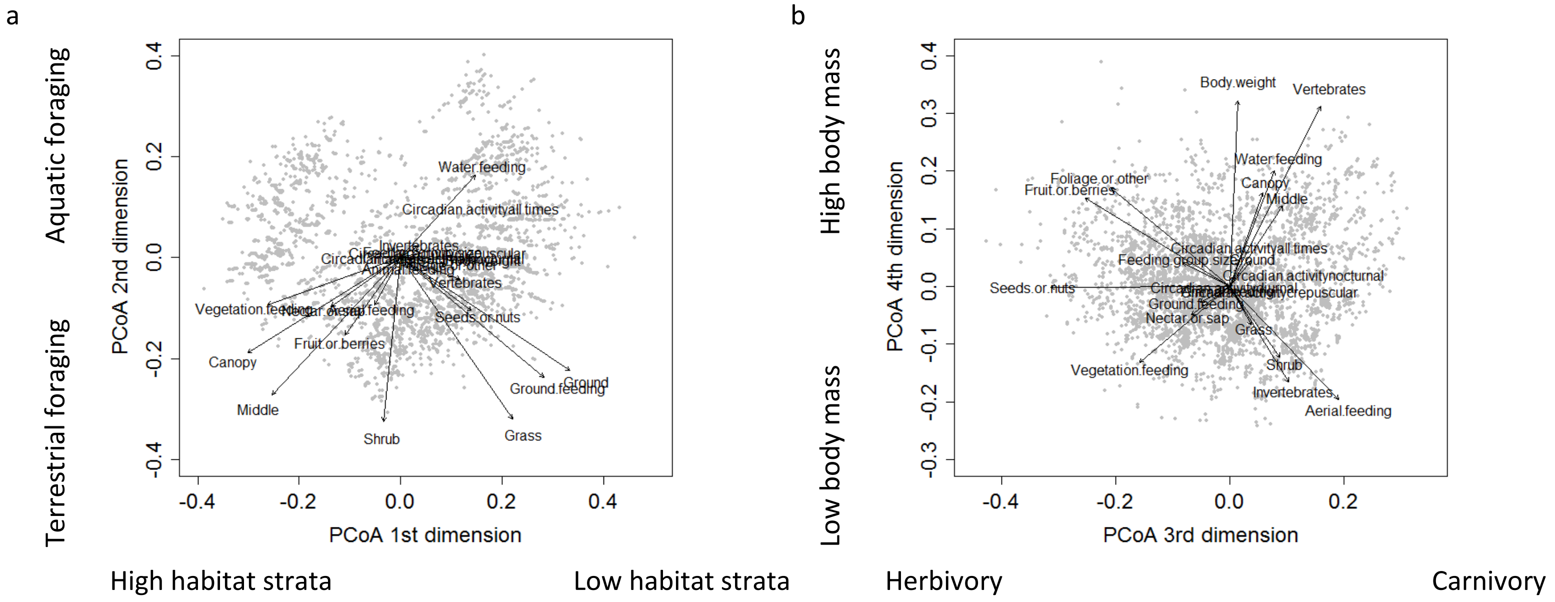

Figure 3.2: Dimensions (a) one and two and (b) three and four of the Principal Coordinates Analysis (PCoA) of species' functional traits related to resource use. Each point is one species in functional trait space. Higher scores of dimension one are associated with lower habitat strata (ground to grass/low vegetation) and feeding on the ground. Lower scores are associated with higher habitat strata (middle layers to canopy or higher) and feeding on vegetation. Higher scores of dimension two are associated with foraging in or on water. Higher scores of dimension three are associated with foraging in the air and feeding on vertebrates. Lower scores are associated with herbivory. Higher scores of dimension four are associated with higher body mass and feeding on vertebrates. Lower scores are associated with aerial insectivores.

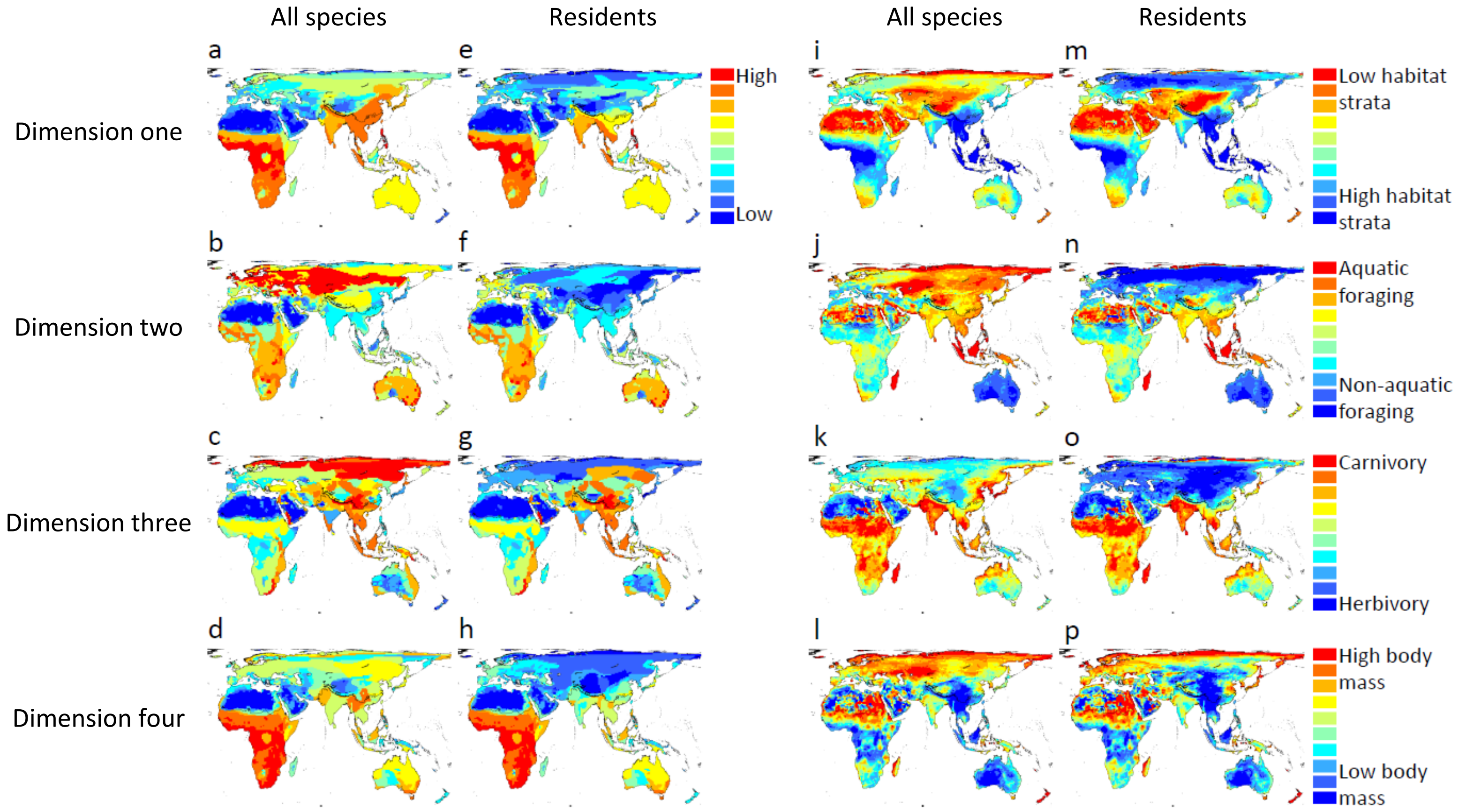

Figure 3.3: Range of PCoA dimension scores for (a-d) all species and (e-h) resident species and mean score of PCoA dimensions for (i-l) all species and (m-p) resident species. The data are divided into deciles in the legend. Dimension descriptions are as described in Figure 3.2.

As expected from its relationship with functional richness (Supplementary Figure 4), species richness showed highly significant quadratic relationships with functional richness in final multivariate models, explaining 49.9% of variation for all species and 38.4% for residents (Table 3.1, Figure 3.1c). Biogeographic realm was also an important factor in final models, explaining more variance for resident species (19.7%) than for all species (11.5%) suggesting a stronger signature of historical biogeographic influences on resident assemblages than migratory assemblages. However, measured historical variables explained very little variance for functional richness (or for the separate trait dimensions), so there may be historical processes that have affected the distribution of functional richness that have not been identified by these models. In Chapter two, contemporary variables were also found to be more important in explaining the distribution of FD.

Precipitation was the most important contemporary predictor of functional richness for all breeding species and residents only (Table 3.1, Figure 3.1c), while temperature and NDVI were also important predictors of functional richness for resident species. The positive associations between precipitation and temperature with functional richness suggests support for the productive energy hypothesis in explaining the latitudinal distribution of functional richness. This is consistent with previous findings that productive energy is important in explaining species richness distributions both for bird assemblages (Hawkins *et al.*, 2003b; Ding *et al.*, 2006; Davies *et al.*, 2007a) as well as a variety of other taxa (e.g. mammals, Tognelli & Kelt, 2004; lepidoptera, Kerr *et al.*, 1998). Contrary to this explanation is the negative association between NDVI and functional richness for resident species. However, NDVI was not significant in the univariate model (Supplementary Table 4) and visual inspection of the distribution of functional richness shows areas of high NDVI with high functional richness of resident species, such as rainforest in the Afrotropics (Figure 3.1b), so its contribution to the final multivariate model should be interpreted with caution. One interpretation of this result is that the relationship with precipitation is non-linear and there is therefore an interaction between these two terms causing the relationship with NDVI to appear negative. The positive relationships with precipitation and temperature may also be signalling stronger environmental filtering in very arid or very cold regions restricting the range of traits that permit survival. Low precipitation was also associated with low functional richness in European fish communities, which was thought to be a response by communities to environmental harshness (Schleuter *et al.*, 2012).

Table 3.1: Parameter estimates (±SE) for the minimum adequate models (MAMs) of predictors of functional richness (volume of functional trait space occupied). Significance values: ** < 0.0001, *** <0.001, ** <0.01, * <0.05, NS Non-significant. ^{a} Zero by default, i.e. intercept.**

	Variable	All species	Residents
Contemporary	**Mean temperature**	+0.0177 (±0.0051)***	+0.0827 (±0.0054)****
	Total precipitation	+0.0513 (±0.0065)****	+0.0510 (±0.0082)****
	Mean NDVI	-	-0.0143 (±0.0033)****
	Temperature seasonality	+0.0538 (±0.0069)****	-
	Cropland extent in 2000AD	-	+0.0036 (±0.0020) NS
Historical	**Temperature change velocity since LGM**	-0.0033 (±0.0022) NS	-0.0234 (±0.0025)****
	Precipitation change velocity since LGM	+0.0090 (±0.0029)**	-
	Duration of cropland	+0.0026 (±0.0010)**	+0.0037 (±0.0013)**
	Duration of grassland	+0.0034 (±0.0012)**	-
Covariates	**Realm: Afrotropics**	0^a	0^a
	Realm: Australasia	+0.0095 (±0.0041)*	+0.0191 (±0.0045)****
	Realm: IndoMalaya	-0.0108 (±0.0026)****	-0.0105 (±0.0032)**
	Realm: Palaearctic	-0.0128 (±0.0018)****	-0.0116 (±0.0022)****
	Area	-0.0015 (±0.0008) NS	-0.0013 (±0.0011) NS
	Species richness	+0.4273 (±0.0113)****	+0.5429 (±0.0143)****
	Species richness²	-0.3422 (±0.0114)****	-0.4481 (±0.0145)****
	AIC	-59693	-53709
	Variance explained	0.945	0.949

The final multivariate models for the range of each of the four trait dimensions had high explanatory power (78.0%-92.6% of variance explained; Table 3.2). The models for the mean values of the dimension also explained a high proportion of the variance (up to 89.9%), although the variance explained by the models for all species for dimensions three and four was lower (47.1% and 59.0% respectively; Table 3.3). Since a positive association with precipitation was a key feature of the interpretation of the correlates of functional richness, it is not surprising that precipitation also shows positive associations with the range of values for a number of the trait dimensions. High precipitation was associated with a greater range of habitat strata (greater range of dimension one), with mean values towards higher habitat strata (lower dimension one scores; Table 3.2, Table 3.3, Figure 3.4). High precipitation is particularly found in tropical rainforest areas whereas low precipitation is associated with shrublands or grasslands (Tucker *et al.*, 1985). Such lack of structural complexity means the latter habitats predictably cannot support species that are active and forage in higher (forest-associated) habitat strata.

Table 3.2: Parameter estimates (±SE) for the minimum adequate models (MAMs) of predictors of the range of PCoA dimension scores. Dimension descriptions are as described in Figure 3.2. Significance values: ** < 0.0001, *** <0.001, ** <0.01, * <0.05, NS Non-significant. ^{a} Zero by default, i.e. intercept. Dimension descriptions are as described in Figure 3.2.**

	Variable	Dimension one		Dimension two		Dimension three		Dimension four	
		All species	Residents	All species	Residents	All species	Residents	All species	Residents
Contemporary	**Mean temperature**	+0.6106 (±0.1005)****	+0.2452 (±0.0166)****	-0.2389 (±0.1201)*	-	-0.9845 (±0.1053)****	+0.0236 (±0.0112)*	-0.2134 (±0.1138) NS	+0.1580 (±0.0116)****
	Total precipitation	+0.8363 (±0.1322)****	+0.1388 (±0.0221)****	-	-0.0458 (±0.0179)*	+0.7799 (±0.1367)****	+0.0938 (±0.0146)****	-	+0.0789 (±0.0154)****
	Mean NDVI	-0.0775 (±0.0473) NS	-0.0259 (±0.0083)**	+0.1288 (±0.0574)*	-	-0.1531 (±0.0531)**	-0.0056 (±0.0056) NS	-	-0.0104 (±0.0055) NS
	Temperature seasonality	+0.3966 (±0.1411)**	+0.1415 (±0.0219)****	+1.2122 (±0.1554)****	-0.1208 (±0.0176)****	+0.3209 (±0.1326)*	+0.0707 (±0.0142)****	-1.1737 (±0.1615)****	+0.0627 (±0.0162)***
	Precipitation seasonality	-	-	+0.2326 (±0.1026)*	-	-	+0.0259 (±0.0091)**	-	-
	NDVI seasonality	+0.1342 (±0.0384)***	+0.0381 (±0.0069)****	-	-	-	-	-	+0.0441 (±0.0045)****
	Number of landcover types	-0.0444 (±0.0279) NS	-	+0.0723 (±0.0377) NS	-	-	-0.0066 (±0.0035) NS	-	-0.0056 (±0.0032) NS
	Human population density in 2000AD	-	-	-	-	+0.0561 (±0.0273)*	+0.0104 (±0.0030)***	-	-
	Cropland extent in 2000AD	-	-	-	+0.0098 (±0.0046)*	-0.1633 (±0.0347)****	-0.0086 (±0.0037)*	+0.0594 (±0.0332) NS	-
	Grassland extent in 2000AD	-	-	-	-	-0.0879 (±0.0259)***	-0.0052 (±0.0027) NS	-	-
Historical	**Temperature change velocity since LGM**	-0.0709 (±0.0375) NS	-0.0657 (±0.0066)****	+0.1490 (±0.0491)**	-	+0.2496 (±0.0419)****	-0.0107 (±0.0044)*	+0.1090 (±0.0436)*	-0.0366 (±0.0044)****
	Median arrival of humans	-	-	+0.1089 (±0.0531)*	-	-0.2120 (±0.0448)****	-	-0.0700 (±0.0476) NS	-
	Duration of cropland	-	-	+0.0641 (±0.0239)**	+0.0084 (±0.0030)**	-	+0.0077 (±0.0022)***	-	-
	Duration of grassland	+0.0361 (±0.0226) NS	-	-	-0.0073 (±0.0038) NS	-	-	-0.0551 (±0.0262)*	-
Covariates	**Realm: Afrotropics**	0^a	0^a	0^a	0^a	0^a	0^a	0^a	0^a
	Realm: Australasia	-0.0809 (±0.0867) NS	+0.0465 (±0.0122)***	+0.3237 (±0.0937)***	+0.0330 (±0.0115)**	+0.0510 (±0.0755) NS	+0.0300 (±0.0081)***	-0.6658 (±0.1045)****	-0.0078 (±0.0099) NS
	Realm: IndoMalaya	-0.0911 (±0.0507) NS	-0.0399 (±0.0085)****	-0.1585 (±0.0633)*	-0.0229 (±0.0079)**	+0.0353 (±0.0530) NS	-0.0061 (±0.0056) NS	-0.1775 (±0.0590)**	-0.0240 (±0.0059)****
	Realm: Palaearctic	-0.1015 (±0.0338)**	-0.0328 (±0.0058)****	-0.1114 (±0.0431)**	-0.0235 (±0.0054)****	-0.0804 (±0.0362)*	-0.0078 (±0.0038)*	-0.0813 (±0.0393)*	-0.0098 (±0.0039)*
	Area	-0.0013 (±0.0157) NS	-0.0049 (±0.0028) NS	-0.0846 (±0.0211)***	-0.0193 (±0.0026)****	+0.0013 (±0.0191) NS	+0.0023 (±0.0020) NS	+0.0070 (±0.0181) NS	-0.0052 (±0.0018)**
	Species richness	+5.2223 (±0.2207)****	+1.1961 (±0.0368)****	+6.2659 (±0.2659)****	+0.6404 (±0.0342)****	+1.7396 (±0.2306)****	+0.4524 (±0.0247)****	+3.2463 (±0.2469)****	+0.6500 (±0.0256)****
	Species richness^2	-3.7194 (±0.2173)****	-1.0245 (±0.0373)****	-4.9480 (±0.2710)****	-0.5240 (±0.0347)****	-0.1253 (±0.2339) NS	-0.3271 (±0.0249)****	-1.0597 (±0.2479)****	-0.5050 (±0.0252)****
	AIC	-2173.4	-35818	3315.6	-37559	170.82	-43957	640.21	-44330
	Variance explained	0.909	0.926	0.820	0.835	0.780	0.833	0.877	0.913

Table 3.3: Parameter estimates (±SE) for the MAMs of predictors of mean PCoA dimension scores. Dimension descriptions are as described in Figure 3.2. Significance values: ** < 0.0001, *** <0.001, ** <0.01, * <0.05, NS Non-significant. ^{a} Zero by default, i.e. intercept. Dimension descriptions are as described in Figure 3.2.**

	Variable	Dimension one		Dimension two		Dimension three		Dimension four	
		All species	Residents	All species	Residents	All species	Residents	All species	Residents
Contemporary	**Mean temperature**	-0.0516 (±0.0044)****	-0.0218 (±0.0049)****	-0.0478 (±0.0046)****	-0.0436 (±0.0049)****	+0.0274 (±0.0037)****	-	-0.0079 (±0.0031)*	-0.0291 (±0.0038)****
	Mean precipitation	-0.0798 (±0.0058)****	-0.0604 (±0.0065)****	-0.0674 (±0.0060)****	-0.0600 (±0.0063)****	+0.0335 (±0.0051)****	-	-0.0157 (±0.0038)****	-0.0314 (±0.0049)****
	Mean NDVI	-0.0092 (±0.0019)****	-0.0077 (±0.0022)***	-0.0063 (±0.0020)**	-0.0106 (±0.0024)****	-	-0.0079 (±0.0024)**	-	-0.0074 (±0.0017)****
	Temperature seasonality	-0.0848 (±0.0066)****	-0.0376 (±0.0073)****	-0.1432 (±0.0070)****	-0.1491 (±0.0067)****	-	-0.0838 (±0.0066)****	-0.0333 (±0.0046)****	-0.0986 (±0.0057)****
	Precipitation seasonality	+0.0158 (±0.0035)****	+0.0206 (±0.0039)****	-	-	-	-	+0.0045 (±0.0026) NS	-
	NDVI seasonality	-0.0093 (±0.0016)****	-0.0111 (±0.0018)****	-0.0155 (±0.0017)****	-0.0268 (±0.0019)****	-	-	-	-0.0119 (±0.0014)****
	Number of landcover types	-0.0022 (±0.0011)*	-	-	-	-	-0.0035 (±0.0016)*	-0.0018 (±0.0009)*	-0.0022 (±0.0010)*
	Human population density in 2000AD	-	-	-	-	-	-	-0.0020 (±0.0007)**	-0.0025 (±0.0009)**
	Cropland extent in 2000AD	-	-	+0.0029 (±0.0012)*	+0.0037 (±0.0015)*	-	+0.0043 (±0.0016)**	+0.0027 (±0.0009)**	+0.0035 (±0.0011)**
	Grassland extent in 2000AD	-	+0.0017 (±0.0010) NS	-	-	-	-	-	-
Historical	**Temperature change velocity since LGM**	+0.0230 (±0.0017)****	+0.0130 (±0.0019)****	+0.0172 (±0.0016)****	+0.0123 (±0.0019)****	-	+0.0068 (±0.0019)***	+0.0076 (±0.0011)****	+0.0135 (±0.0014)****
	Precipitation change velocity since LGM	-0.0082 (±0.0022)***	-0.0087 (±0.0025)***	-	-	+0.0074 (±0.0023)**	-	-	-
	Duration of cropland	-0.0041 (±0.0007)****	-0.0046 (±0.0008)****	-	+0.0018 (±0.0009) NS	-	+0.0033 (±0.0010)**	-0.0010 (±0.0005) NS	-
	Duration of grassland	-0.0034 (±0.0009)***	-0.0017 (±0.0010) NS	-0.0036 (±0.0010)***	-0.0046 (±0.0011)****	-	-0.0059 (±0.0013)****	-0.0027 (±0.0007)****	-0.0039 (±0.0008)****
Covariates	**Realm: Afrotropics**	0^a	0^a	0^a	0^a	0^a	0^a	0^a	0^a
	Realm: Australasia	-0.0547 (±0.0051)****	-0.0465 (±0.0051)****	-0.0177 (±0.0051)***	-0.0065 (±0.0039) NS	-0.0082 (±0.0033)*	-0.0004 (±0.0043) NS	+0.0081 (±0.0030)**	-0.0003 (±0.0039) NS
	Realm: IndoMalaya	+0.0087 (±0.0021)****	+0.0057 (±0.0024)*	+0.0030 (±0.0022) NS	+0.0086 (±0.0025)***	+0.0011 (±0.0023) NS	+0.0054 (±0.0028) NS	-0.0011 (±0.0016) NS	+0.0015 (±0.0019) NS
	Realm: Palaearctic	+0.0026 (±0.0014) NS	+0.0013 (0.0016) NS	-0.0025 (±0.0015) NS	+0.0003 (±0.0017) NS	-0.0004 (±0.0015) NS	-0.0007 (±0.0019) NS	-0.0005 (±0.0010) NS	+0.0007 (±0.0012) NS
	Area	-0.0029 (±0.0006)****	-0.0040 (±0.0007)****	-0.0047 (±0.0007)****	-0.0073 (±0.0008)****	-0.0026 (±0.0007)***	-0.0047 (±0.0009)****	-0.0043 (±0.0005)****	-0.0055 (±0.0006)****
	AIC	-64983	-62556	-63717	-60650	-62066	-58283	-70984	-67180
	Variance explained	0.899	0.833	0.896	0.890	0.471	0.751	0.590	0.858

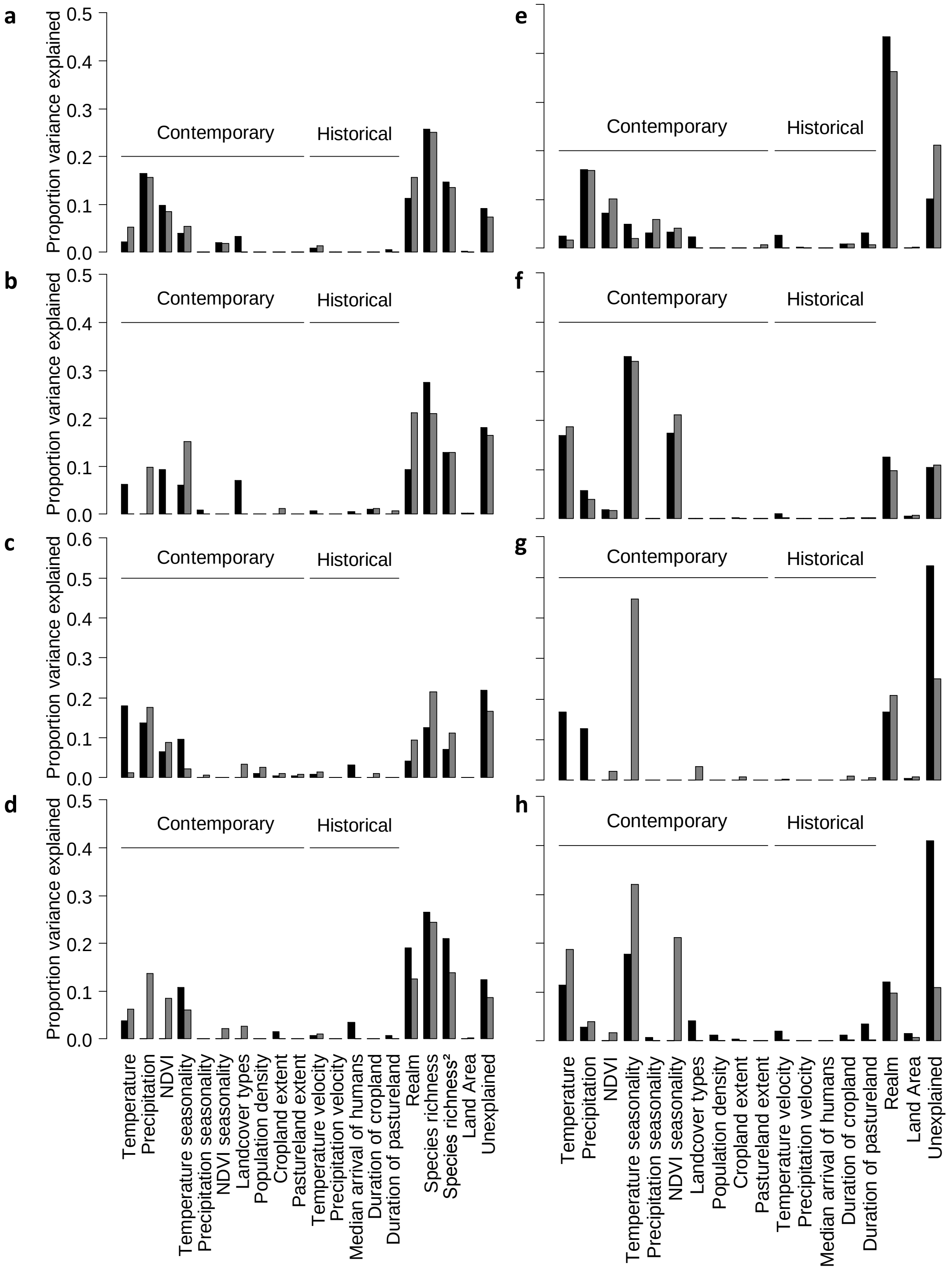

Figure 3.4: The relative importance of predictors as determined by hierarchical partitioning in the final models for range (a-d) and mean (e-h) of PCoA dimension one (a & e), two (b & f), three (c & g) and four (d & h) for all birds (black bars) and resident birds (grey bars). Dimension descriptions are as described in Figure 3.2.

High precipitation was also associated with a greater trophic range (greater range of dimension three) and higher average trophic position (higher dimension two scores; Table 3.2, Table 3.3, Figure 3.4). Additionally, temperature had a negative association with trophic range for all species, but was only marginally important for residents only. Therefore, during the breeding season there is a higher trophic range in cooler areas, indicating that migratory species that breed at high latitudes are making use of seasonally-available animal food resources that are not available during the winter months. Temperature also had a positive association with the mean value of this dimension, with species on average feeding at higher trophic levels in warmer regions. These findings are consistent with both the productive and ambient variants of the energy hypothesis for the distribution of biodiversity; productive energy may increase diversity partly through food chain lengths being greater in areas of higher productivity (Elton, 1927), while regions of low ambient energy may limit the availability of flying insect prey.

Regions of low temperature were associated with larger body size (lower dimension four scores). This finding supports Bergman's (1847) rule that larger species are found in colder environments (and higher latitudes), and is consistent with Olson *et al.*'s (2009) finding that temperature was significantly negatively associated with body size in birds. This is because temperature sets a minimum size for endotherms in order that they can maintain a constant temperature (Blackburn & Gaston, 1994) providing an additional mechanism underpinning the ambient energy hypothesis.

Examination of the different trait dimensions also provided some insights into the role of seasonality and environmental stability on diversity patterns. Areas of high temperature seasonality were associated with a greater range of aquatic-terrestrial strategies for all species, but with a restricted range for resident species (range of dimension two; Table 3.2, Figure 3.4). Areas of greater temperature seasonality were less likely to have both breeding and resident birds that use aquatic habitats for foraging (lower dimension two scores; Table 3.3, Figure 3.4). Resident species are restricted in the availability of aquatic niches in highly seasonal areas during the winter because many wetland areas at high latitudes are frozen over. Millions of shorebirds and waterfowl migrate between the Palaearctic and sub-Saharan Africa, and the time of their migration can be affected by the timing of freeze-up (Newton, 2008).

Areas of high temperature seasonality were associated with a greater trophic range, though this relationship was stronger and more important when migratory species were included (greater range of dimension three; Table 3.2, Figure 3.4). Resident species of highly seasonal areas were more likely to occur in the herbivorous region of trait space (lower dimension three scores; Table 3.3, Figure 3.4). For species breeding above 35°N, the majority of species that migrate south for the non-breeding season are insectivorous (and these species migrate further towards less seasonal habitats), since seeds and fruits are much more readily available to those species that remain during the winter months than insect food (Newton, 2008).

3.5 Conclusions

The evidence presented here suggests that the distribution of functional richness of bird assemblages across the Old World largely reflects contemporary environmental gradients in terms of both the distribution of productive energy (indicated by the positive relationships with precipitation and temperature) and filtering effects of harsh environmental conditions (very cold and/or dry regions). Consideration of each of the main trait dimensions separately also indicates the important role of the productive energy hypothesis in explaining latitudinal diversity gradients (e.g. more productive areas were associated with a greater range of habitat strata and of trophic levels). It also provided insights into the importance of the ambient temperature hypothesis (e.g. colder temperatures were associated with larger body size and fewer species feeding at higher trophic levels), which may be masked in a composite measure like functional richness. There was little support for the habitat heterogeneity hypothesis, with no significant relationships with number of landcover types in the multivariate models for functional richness or the range of trait dimensions, and only marginally significant relationships that explained a very small proportion of the variance for models of the mean values of trait dimensions.

Chapter Four: Seasonal changes in avian functional diversity as a result of migration

4.1 Abstract

Aim: Migration generates significant composition change for bird communities each year. This study investigates how the macroecological distribution of functional diversity - the variety of traits that influence ecosystem functioning - changes between seasons as a result.

Location: The Palaearctic-Afrotropical Migration Flyway

Methods: Functional traits related to resource use are used to ordinate in multidimensional trait space the 2,310 bird species that occur in the Afrotropics and/or the Western Palaearctic in the breeding and/or non-breeding seasons. The volume of this trait space (functional richness) and the regularity of species within it (functional evenness) are used to quantify functional diversity. These functional diversity metrics are calculated for approximately one-degree grid cells for the breeding and non-breeding seasons. Taxonomic dissimilarity between seasons (change in species present) is compared to functional dissimilarity (change in functional space occupied between seasons). Functional diversity is also calculated for defined functional groups – terrestrial predators, insectivores and herbivores, and aquatic foragers.

Results: Functional richness, which ranges from 0 to 0.33, declines by between 0.08 and 0.17 in the cells across the northern Palaearctic in the non-breeding season, whereas the majority of cells across the Afrotropics change by less than 0.02 between seasons. In regions of the Afrotropics receiving most migratory species (up to 164 in some cells), functional evenness, which ranges from 0.13 to 0.90 in this region, is lower in the non-breeding season than the breeding season. The functional evenness of most cells in the Afrotropics decrease by up to 0.04 in the non-breeding season, while some decrease by up to 0.32; species are more clustered in functional space. Taxonomic and functional dissimilarity between seasons both vary between 0 and 1 (i.e. complete similarity to complete dissimilarity of assemblages), but functional dissimilarity is lower than taxonomic dissimilarity in most cells; the majority of cells have functional dissimilarity less than 0.2, whereas the majority of cells have taxonomic dissimilarity greater than 0.2.

Main conclusions: The seasonal change in functional diversity suggests the non-breeding assemblages are affected by environmental filtering at high latitudes (manifested differently by functional groups, e.g. predators and insectivores may be limited by prey availability whereas aquatic foragers are limited by foraging habitat) and increased niche partitioning in the tropics. Migratory birds contribute to functional diversity in their breeding and wintering grounds. They therefore require protection across their annual range; at some sites they may show high redundancy but their functional importance may change seasonally.

Keywords: Competition, dissimilarity, environmental filtering, functional evenness, functional richness, herbivores, insectivores, Palaearctic-Afrotropical Flyway, predators, resource partitioning, species packing, water birds.

4.2 Introduction

A distinctive feature of avian communities is that the majority experience significant seasonal species turnover as a result of migration. Birds are the taxon in which migratory behaviour is most widespread (Newton, 2008); many bird species migrate to lower latitudes (or altitudes) in search of more benign conditions during the winter months. The question of how community structure is changed by migrants that integrate into year-round resident communities of tropical regions has often been discussed (e.g. Moreau, 1972; Leisler, 1992; Poulin & Lefebvre, 1996; Mönkkönen & Forsman, 2005; Salewski & Jones, 2006).

In this study, the changing macroecological distribution of biodiversity due to migratory species is investigated by considering the ecological traits that describe species' resource use. These traits are used to calculate functional diversity, defined as "the value and range of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001). Functional diversity has been used to understand the assembly of ecological communities of birds and other taxa (e.g. Petchey *et al.*, 2007; Mendez *et al.*, 2012; Mouillot *et al.*, 2007; Thompson *et al.*, 2009). By considering functional diversity as "the distribution of the species and abundance of a community in niche space", a number of metrics can be calculated that characterise different components of functional diversity (Mason *et al.*, 2005). Functional richness is the volume of niche space occupied and functional evenness measures the regularity of the distribution of species within the space. Functional evenness is lower when distances between species in niche space are less regular, i.e. species exhibit clustering and some areas of niche specie are not fully utilised. If species abundances are also taken into account, functional evenness is lower when those abundances are unevenly distributed in niche space.

In some regions, migratory species may occupy habitats in which they are not in direct competition with resident species because they belong to a separate ecological guild. For example, Western Africa is relatively depauperate in terms of water birds and the ten sandpiper species (Scolopacidae) that migrate to Northern Nigeria do not encounter any members of their own family in their wintering grounds (Moreau, 1972). If the combination of traits represented by these migratory species falls outside of the volume of niche space occupied by resident species, these sandpipers will increase functional richness in their wintering grounds. Alternatively, if the ecological position of migratory species is within the overall volume of niche space occupied by resident species, but fills a gap in a relatively underused part of that space, the arrival of these species will not change functional richness but will increase functional evenness by increasing the overall regularity of species in niche space. As well as comparing the functional richness and evenness of the assemblages in each season, the proportion of niche space occupied in each season that is non-overlapping can be used to quantify functional dissimilarity (Villéger *et al.*, 2011). High functional dissimilarity between seasons may indicate that ecosystem processes are subject to considerable change throughout the year. The movement of birds with particular traits between different areas may mean that migratory species contribute to ecosystem processes in ways that resident species alone could not.

Some migratory species may join communities of resident species that have similar niches to their own, resulting in inter-specific competition and resource partitioning. The latter is possible when species have narrower niche breadths so that niche overlap is limited. There are many examples of resource partitioning between resident and migrant species; for example, a comparison of two insectivorous Palaearctic migrants – pied flycatcher (*Ficedula hypoleuca*) and willow warbler (*Phylloscopus trochilus*) – with Afrotropical residents, suggested that resource partitioning allows co-existence of migrants and residents in the same guild and is exhibited in these species through differences in foraging techniques and substrates (Salewski *et al.*, 2003). An influx of additional species with narrow niche breadths may increase resource partitioning and cause a decrease in functional evenness since species may be specialising on very similar resources and therefore cluster in functional space.

Some theories of the ecological differences contributing to resource partitioning between residents and migrants have been suggested (reviewed by Leisler, 1992; Salewski & Jones, 2006). It has been proposed that migrant species make more use of ephemeral or seasonal food resources, have a higher foraging rate, use their wings more often for foraging, forage higher and in more open habitats and use a greater range of foraging techniques. However, there are many accounts of contradictory results and it is difficult to draw generalisations for how migrants fit into resident communities (Salewski & Jones, 2006). Understanding the competitive relationships between migrants and residents is of conservation importance since migrants are declining at a faster rate than their non-migratory taxonomic counterparts (Sanderson *et al.*, 2006) and these competitive relationships are likely to change as a result of climate change (Lemoine & Böhning-Gaese, 2003; Ahola *et al.*, 2007).

Here we use the Palaearctic-Afrotropical migration as a case study to investigate this issue at a macroecological scale. Each year, billions of birds migrate from the Palaearctic to the Afrotropics (Moreau, 1972); a recent estimate put the number at 2.1 billion passerines and near-passerines crossing the Sahara each year from Europe (Hahn *et al.*, 2009), as well as other groups such as water birds and raptors. Functional diversity measures that represent functional richness and evenness are calculated for the assemblages of the Afrotropics and the Western Palaearctic region, where the majority of Afrotropical migrants breed (Moreau, 1972), for the breeding and non-breeding seasons. The change in these measures between seasons is used to make inferences about the change in community composition between seasons both in assemblages receiving migrants and those from which birds emigrate. Functional dissimilarity between seasons is calculated to assess whether there is a change in the functional space occupied, i.e. whether the functional space occupied in the two seasons is non-overlapping. The majority of macroecological analyses involving birds use breeding ranges for species' distributions (e.g. Belmaker *et al.*, 2012; Olson *et al.*, 2009). However, macroecological patterns are likely to show significant intra-annual differences. Therefore, these analyses also give an indication of the seasonal change in biodiversity patterns. Additionally, analyses will be conducted for defined functional groupings based on foraging ecology; different groups may change functional richness or evenness in different ways depending on the distribution of resident species and the degree of interspecific competition and/or resource partitioning. The implications for future changes in population sizes and geographical ranges of migratory species and for prioritising conservation efforts are discussed.

4.3 Methods

4.3.1 Distribution of bird species

The geographic extent of the study area consists of the Afrotropical region and the Western Palaearctic. The Eastern Palaearctic was excluded beyond 60° East, where the Ural mountains form a natural geographic barrier to migration (Moller *et al.*, 2011) and since the majority of Afro-tropical migrants breed in the West and Central Palaearctic (Moreau, 1972). Thus the regional pool consisted of 2,310 species that occur in the Afrotropics and/or the Western Palaearctic during the breeding and/or non-breeding season.

Species were classified as being a “Full Migrant”, an “Altitudinal Migrant”, “Nomadic” or “Not a Migrant” in the BirdLife International database. Of the 2,310 species, 570 were classed as full migrants and 1,656 were not migratory. Of the fully migratory species, 95 had both the breeding and non-breeding distributions within the Afrotropics, 136 had both distributions within the Palaearctic and 38 had their breeding distributions within the Palaearctic and their non-breeding distributions within the Afrotropics. The remaining 301 migratory species did not fit into one of these categories; for example, some had breeding and non-breeding distributions in the Afrotropics as well as breeding distributions in the Palaearctic. Of the species that are not migratory, 1,572 were resident in the Afrotropics and 257 were resident in the Palaearctic (and 173 of these were resident in both realms).

Analyses of distributions were carried out using ArcMap 9.3 (ESRI, 2010). Shape files of bird species ranges were provided by BirdLife International (Birdlife International & Natureserve, 2011). These maps are most complete and accurate current estimates of Extent of Occurrence maps for all extant bird species and have been produced using known locations (e.g. geo-referenced point locality records, collecting locality of museum specimens) and expert opinion (see Buchanan *et al.* (2011) for details). For each species, the areas in which it is considered extant or probably extant through the year or the breeding season or non-breeding season were included. Areas where a species was considered possibly extant or possibly extinct or where its presence was uncertain were excluded. Sea birds, defined as those species which predominately feed at sea and are described as pelagic or feeding offshore (Del Hoyo *et al.*, 1992; 1996), were excluded from the analysis. The exclusion criteria were consistent with those used in other macroecological analyses of bird distributions (e.g. Orme *et al.*, 2006; Hurlbert & Jetz, 2007).

The range maps of birds present in the Afrotropics and the Palaearctic west of 60° East (Olson *et al.*, 2001) were sampled on a grid using the Behrmann cylindrical equal-area projection. The cell resolution was 96.486 km x 96.486 km, equivalent to 1° longitude and approximately 1° latitude at the 30° latitude of true scale. This created 2,322 cells in the Afrotropics and 2,729 in the Palaearctic where grid cells had >50% land area; each assemblage comprised all those species whose ranges overlapped with the grid cell. Species richness ranged between 1 and 674 in the breeding season (breeding and resident ranges) and between 2 and 749 in the non-breeding season (non-breeding and resident ranges).

4.3.2 Trait data

Traits were selected for their role in resource use in order to calculate the functional diversity of the communities (Table 4.1). Feeding location, strata used and diet were considered as binary traits since the categories are not exclusive. For example, a bird could feed both on the ground and in vegetation. Trait values for each species were collated using a variety of sources (Appendix S1: Sources used for bird trait data). Where data were not available for individual species (<8% of species/trait combinations), genus, or failing that family, values were used (Table 4.1). Overall, 92.3% of the species/trait combinations used were specific to individual species, 7.6% were genus averages and 0.1% were family averages.

Table 4.1: Functional traits used for calculating functional diversity.

Trait		Possible values	% Species-trait combinations using averages	
			Genus	Family
Weight ($\log_e$ grams)	Continuous	1.61-11.62	5.5	0.4
Circadian activity	Categorical	Diurnal / nocturnal / crepuscular / all times	10.6	-
Feeding group size	Ordinal	1 / 2-6 / 6-10 / 10-20 / 20-50 / >50	8.4	-
Feeding location(s)	Ground	Yes/no	6.1	0.4
	Water	Yes/no		
	Vegetation	Yes/no		
	Aerial	Yes/no		
	On other animals	Yes/no		
Strata used	Ground/water	Yes/no	7.8, 11.7*	-
	Grass/low vegetation	Yes/no		
	Shrub layer/understorey	Yes/no		
	Middle layers	Yes/no		
	Canopy or above	Yes/no		
Diet	Vertebrates	Yes/no	3.0	0.1
	Invertebrates	Yes/no		
	Fruit & berries	Yes/no		
	Seeds & nuts	Yes/no		
	Nectar & sap	Yes/no		
	Foliage & other plant parts, e.g. roots	Yes/no		

**7.8% of data on the lowest stratum used and 11.7% of the data on the highest stratum used were genus averages; species are assumed to use all the strata in between their highest and lowest heights.*

4.3.3 Functional diversity

Functional richness and evenness were calculated according to Villéger, Mason & Mouillot (2008). Species are plotted in T-dimensional space, where T is the number of traits (in this case, T= 19; Figure 4.1a). Functional richness (FRic) is the volume of the convex hull that encompasses all the species in the community (Figure 4.1b). The larger the functional space occupied (or the more extreme trait values at the outer edge of the functional space), the greater the functional richness. To calculate functional evenness (FEve), a minimum spanning tree (MST) is created which connects all the species in the community and the regularity of the branch lengths is calculated (Figure 4.1c). FEve varies between 0 and 1; a value of 1 for FEve indicates that the branches of the MST are all of equal length and the species are arranged with perfect regularity within the functional space and low FEve indicates that there is clustering is some part(s) of the functional space. All calculations of functional diversity metrics were carried out using R version 2.12.0 (R Development Core Team, 2010). FRic and FEve were calculated using the FD package (Laliberté & Shipley, 2011).

Figure 4.1: Estimation of the two functional diversity indices in multidimensional functional space. For simplification, only two traits and nine species are considered. (a) The points are plotted in the space according to the trait values of the corresponding species. In (b), the convex hull is drawn with a solid black line; the points corresponding to the vertices are black, and the convex hull volume is shaded in grey. The functional richness (FRic) corresponds to this volume. (c) The minimum spanning tree (MST, dashed line) links the points. Functional evenness (FEve) measures the regularity of points along this tree. For convenience, the tree is plotted stretched under the panel. Figure and caption adapted from Villéger *et al.* (2008).

In order to identify communities where the functional diversity is different from the expected value given the number of species, the observed functional diversity of each community was compared to a null model. The null model assumes neutral community assembly. The original matrix of community (rows) and species (columns) is subjected to a matrix swap randomisation whereby the sums of the columns and rows in the randomisation are equal to the original matrix, i.e. species richness and the number of grid cells occupied by each species across the matrix are kept constant. This is to ensure that rare species do not have a disproportionate influence on the model. The functional diversity of the simulated community is calculated and this is repeated so that 100 randomisations are created for each community. The mean of these randomisations is the expected functional diversity. The difference between the observed and expected values is calculated and divided by the standard deviation of the expected values to calculate a standardised effect size (SES). Matrix swap randomisations were done using the *permatfull* function in the *vegan* package (Oksanen *et al.*, 2011).

Since birds that utilise particular resources may assimilate into resident communities in different ways, we tested the ideas for defined functional groupings based on foraging ecology (Table 4.2). For each of these groups, FRic, SES_{FRic}, FEve and SES_{FEve} were calculated. The traits used to identify the functional groupings were excluded from these calculations.

Table 4.2: Functional groups of bird species used for separate analyses, as defined by feeding and foraging habits.

Functional group	Description	Number of species	Percentage of species that are full migrants
Terrestrial predators	Feed on vertebrates only. Do not forage in/on water.	43	48.8%
Terrestrial insectivores	Feed on invertebrates only. Do not forage in/on water.	664	22.6%
Terrestrial herbivores	Do not feed on vertebrates or invertebrates. Feed on some combination of fruit & berries, seeds & nuts, nectar & sap, foliage & other plant parts. Do not forage in/on water.	180	11.7%
Aquatic foragers	Forage in/on water only.	126	65.9%

4.3.4 Multivariate analysis of functional space

The proportion of functional space that is overlapping between the breeding and non-breeding seasons can be used to measure the functional dissimilarity in the two seasons.

Taxonomic dissimilarity can be measured as the proportion of species not shared by two communities. Recently, a measure of functional dissimilarity has been introduced that measures the proportion of the convex hulls of two communities that does not overlap (Villéger *et al.*, 2011). In the analyses performed in this chapter, if the functional space occupied by species in a given cell in the breeding season is very different from the functional space occupied by the species present in the non-breeding season, then the proportion of overlap of the convex hulls will be low and the functional dissimilarity will be high. Conversely, if the functional space occupied is similar in both seasons, then the proportion of overlap will be high and the functional dissimilarity will be low. Functional dissimilarity can be due to two processes: functional turnover (e.g. the functional space occupied by species in the non-breeding season is different from that occupied in the breeding season) and functional nestedness (e.g. the functional space occupied by the species in the non-breeding season is a subset of the functional space occupied by species in the breeding season) (Villéger *et al.*, 2013). We used a recently developed method to partition the functional dissimilarity into that contribution from functional turnover and that from the nestedness-resultant component (Villéger *et al.*, 2013). Functional dissimilarity was calculated using the *functional.beta.pair* function in the *betapart* package (Baselga *et al.*, 2013).

As a comparison to functional dissimilarity, the dissimilarity of taxonomic composition was also calculated. By comparing the number of species present in a cell in both seasons with the number of species that are only present in one of the seasons, you can generate a value of compositional dissimilarity. This can also be partitioned into the contribution from species turnover and that from the nestedness-resultant component (Baselga, 2010). Taxonomic dissimilarity was calculated using the *beta.pair* function in the *betapart* package (Baselga *et al.*, 2013).

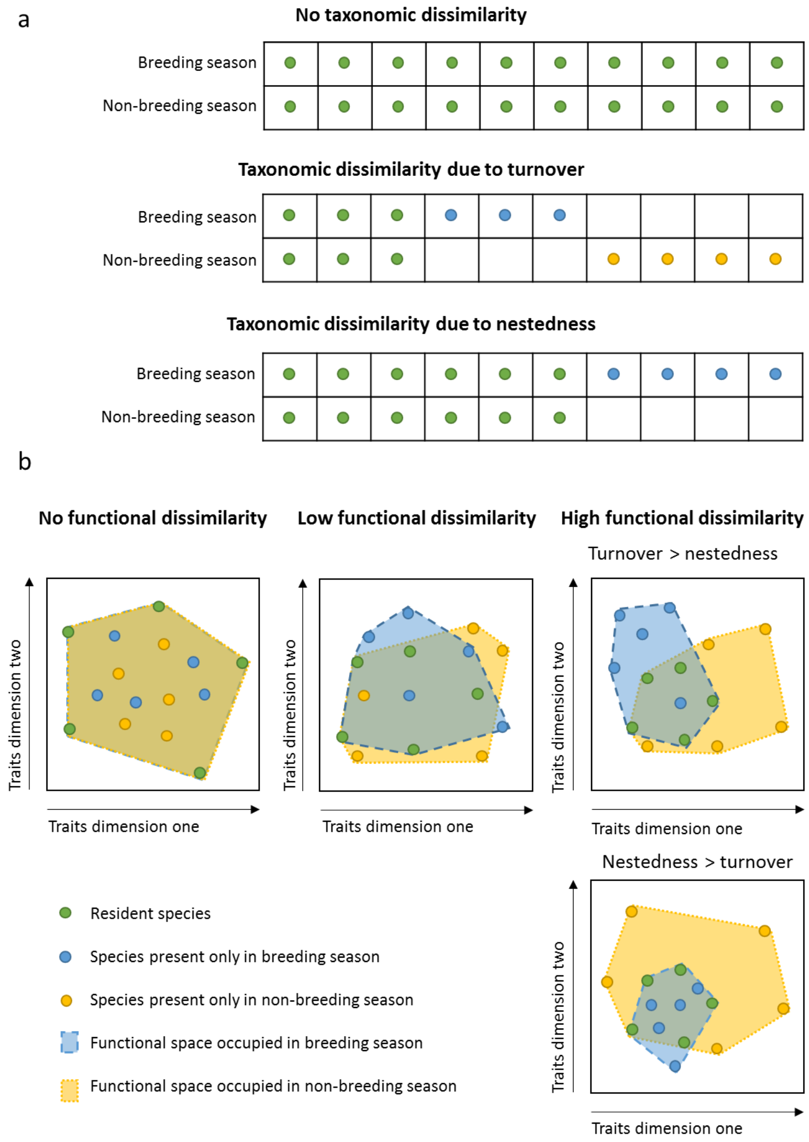

Figure 4.2: A schematic to demonstrate taxonomic and functional dissimilarity. (a) Taxonomic dissimilarity is the proportion of species not shared by two communities. If the same species are present in both seasons, then taxonomic dissimilarity is zero. Taxonomic dissimilarity can either result from turnover – species are present in one season but not the other and vice versa – or nestedness – the species present in one season are a subset of those present in the other. (b) Functional dissimilarity is the proportion of the convex hulls (functional space) of two communities that does not overlap. If the functional space occupied in both seasons is the same, then functional dissimilarity is zero. Functional dissimilarity can either result from turnover – functional space is occupied in one season but not the other and vice versa – or nestedness – the functional space occupied in one season is a subset of that occupied in the other.

Principal Coordinates Analysis (PCoA), also known as multidimensional scaling (Gower, 1966), was used to visualise the distribution of species within the functional space. PCoA is similar to Principal Components Analysis (PCA), but is can be used for traits which are not measured on a continuous scale. The PCoA is used to plot the species so that the distances between them are approximately equal to the dissimilarities in their trait values. The PCoA plots of Afrotropical residents, Palaearctic residents and migrants were compared to the PCoA plot of Indo-Malaya residents as an alternative tropical community to the Afrotropics. There were 1,200 species that were classified as not migratory that had ranges in IndoMalaya. Of these, 40 were also resident in the Afrotropics and 75 were also resident in the Palaearctic (37 were resident in all three realms). PCoA was calculated using the *cmdscale* function.

4.4 Results

In northern latitudes, there were a large number of species that were only present in cells during the breeding season (up to 164 species; Figure 4.3a) representing 70% or more of the species present during the breeding season in grid cells within central continental or northern Palaearctic areas (Figure 4.3b). The species richness in cells at 40° latitude or higher was much greater in the breeding season than the non-breeding season (Supplementary Figure 5). The areas with the highest number of species present only in the non-breeding season included wetland habitats in otherwise seasonally dry environments (e.g. the Nile Delta, the Tigris–Euphrates river system, the Senegal-Gambia Catchments, the Inner Niger Delta and Lake Turkana) and mountainous areas (e.g. the Ethiopian Highlands) (Figure 4.3c). The species migrating into the areas of the Afrotropics with the highest number of species present only in the non-breeding season made up a relatively small proportion of the overall species richness (Figure 4.3d). The proportion of species present only in the non-breeding season was highest in arid areas of North Africa and the Middle East including the Arabian Peninsular (Figure 4.3d).

The functional richness of cells was much lower in the non-breeding season than the breeding season in the northern continental Palaearctic, but the change in functional richness between the two seasons was relatively small across the Afrotropics (Figure 4.4a,e,i). SES_{FRic} was lower in the non-breeding than breeding season in the northern continental Palaearctic (Figure 4.4b,f,j), indicating that the functional richness decreased by a larger amount than would be expected by the decrease in species richness when species emigrate post-breeding. Conversely, the small increase in functional richness in the non-breeding season in parts of the Sahel region was greater than expected by the change in species richness alone, as indicated by the increase in SES_{FRic}.

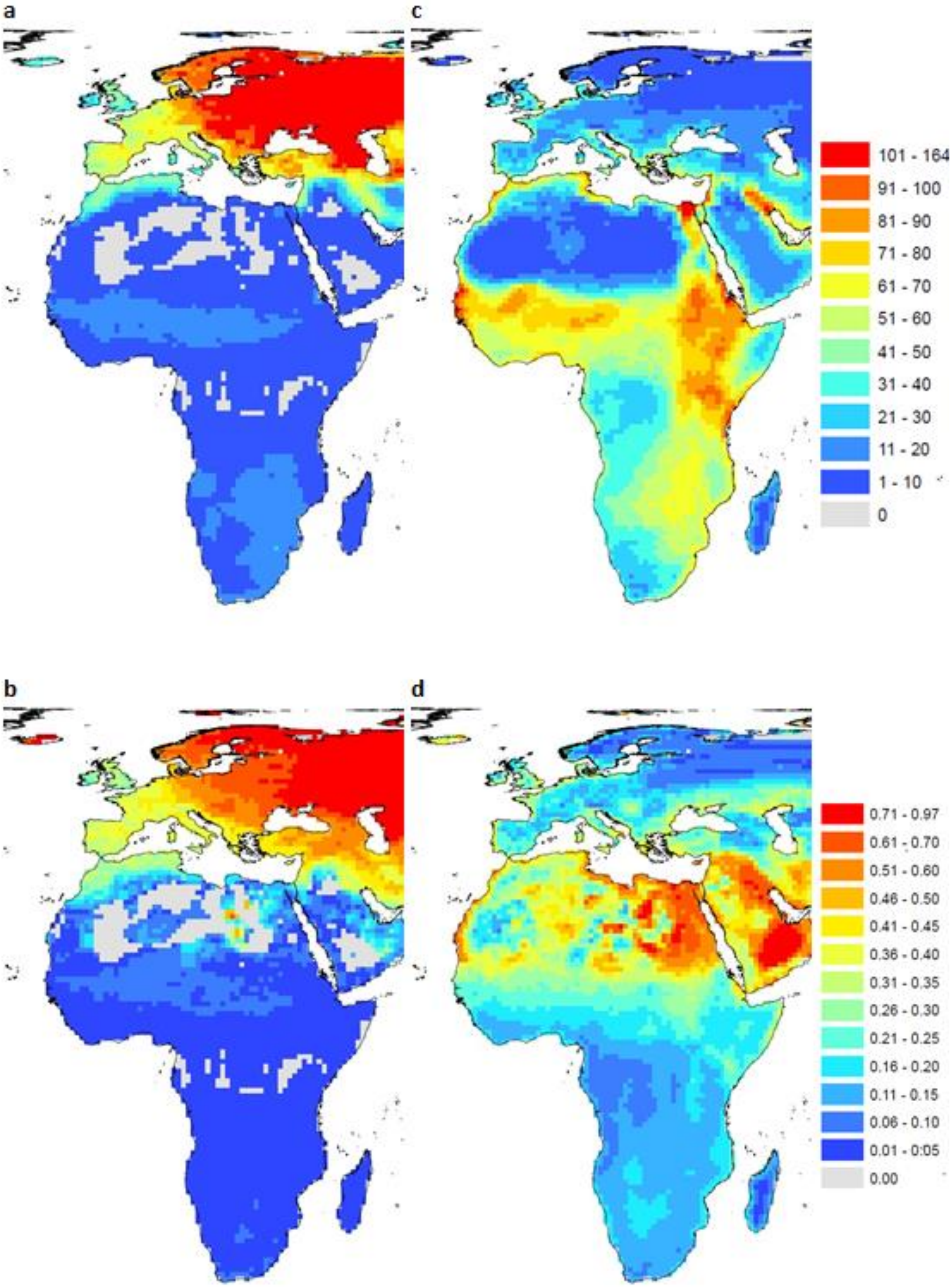

Figure 4.3: The number (a & c) and proportion (b & d) of bird species in an assemblage present only during the breeding season (a & b) and non-breeding season (c & d) in the Afrotropics and Western Palaearctic.

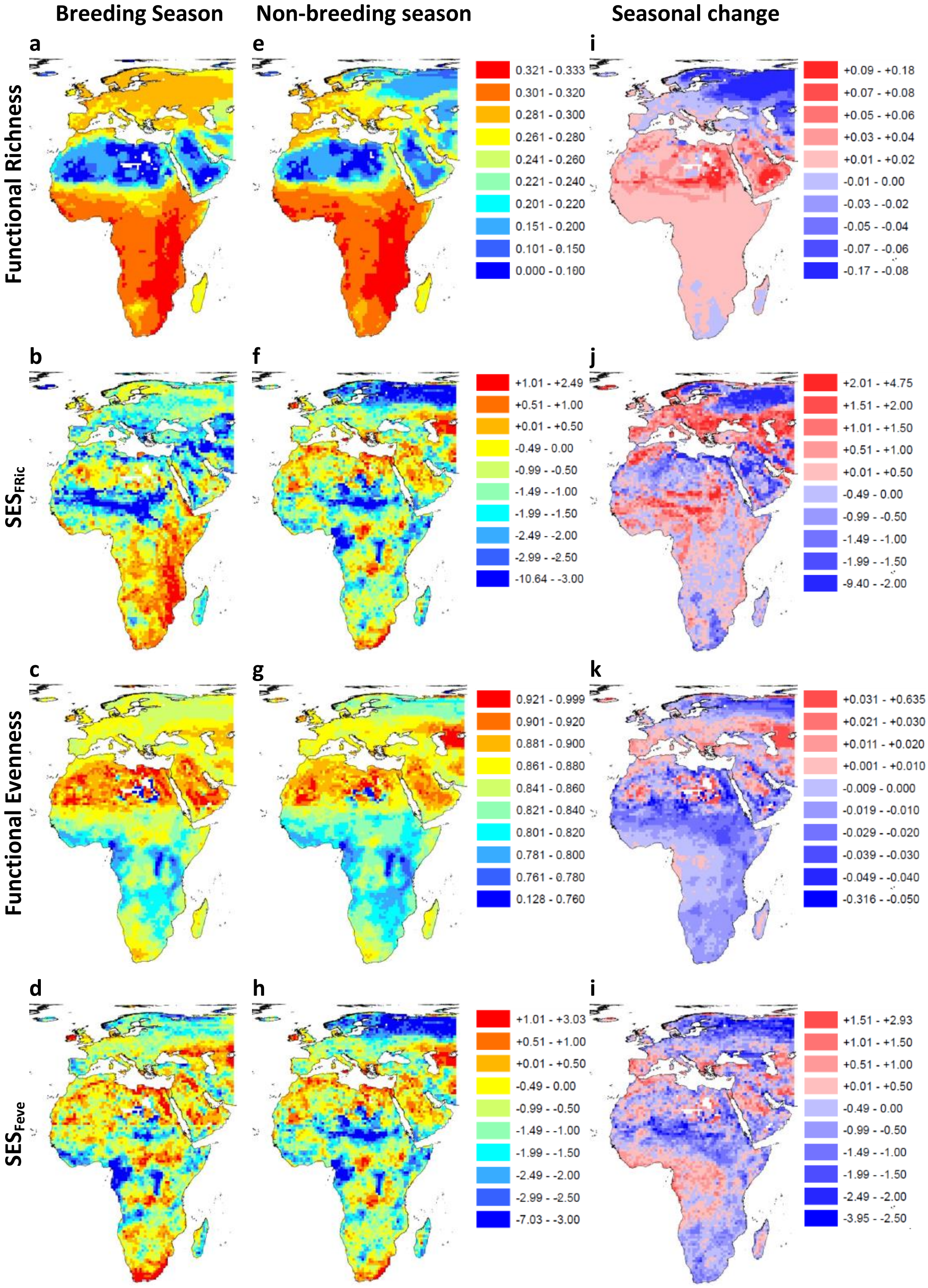

Figure 4.4: The functional richness (FRic) (a & e), Standardised Effect Size of functional richness (SES_{Fric}) calculated using a null model to take account of species richness (b & f), functional evenness (FEve) (c & g) and Standardised Effect Size of functional evenness (SES_{Feve}) (d & h) of assemblages of all species during the breeding season (a-d) and non-breeding season (e-h) and the change in (i) FRic, (j) FEve, (k) SES_{Fric}, (l) SES_{Feve} (non-breeding season minus breeding season). Functional richness measures the volume of functional space occupied and functional evenness measures the regularity of species in functional spaces; see Figure 4.1.

Functional evenness was low across most of the Afrotropics, particularly in the Eastern Arc and the Congo basin (Figure 4.4c,g). In the areas receiving most migratory species, functional evenness was lower in the non-breeding season than the breeding season, indicating that species were more clustered in functional space (Figure 4.4k). The distribution of SES_{FEve} shows that there were some regions in the Afrotropics where species were more clustered in functional space than expected by chance, such as the Sahel and the Congo basin (Figure 4.4d,h). In the Sahel, one of the regions that has the most species present only in the non-breeding season (Figure 4.3c), SES_{FEve} was much lower in the non-breeding season than the breeding season (Figure 4.4l).

The change in species richness for each of the functional groups is shown in Supplementary Figure 6. In both the breeding and the non-breeding seasons, there was high functional richness of terrestrial predators in the Congo Basin (Figure 4.5a,e). SES_{FRic} was high, indicating that the functional richness was greater than expected given the species richness (Figure 4.5b,f). This region also had reasonably high functional evenness (Figure 4.5c), though it was lower in the non-breeding season (Figure 4.5g). After the Congo basin, the region with the next highest functional richness of terrestrial predators in the breeding season was the northern Palaearctic (Figure 4.5a), although there was a sharp decline in functional richness in this region in the non-breeding season (Figure 4.5e,i) and the functional evenness was also low in the non-breeding season (Figure 4.5f). Conversely, the functional richness and evenness increased in southern Europe in the non-breeding season (Figure 4.5i,k). For terrestrial insectivores, functional richness was high and functional evenness low across most of the region in the breeding season (Figure 4.6a,c). However, in the non-breeding season, functional richness was much lower (Figure 4.6e,i) and functional evenness much higher (Figure 4.6g,k) in the Palaearctic. The functional group of terrestrial herbivores had the smallest proportion of migratory species (Table 4.2) and seasonal change in functional diversity was less pronounced than the other groups. Functional richness was low across the Palaearctic in both seasons and the highest functional richness was found in the savannah belt and the East African rift valley (Figure 4.7a,e). For aquatic foragers, highest functional richness was found in Eastern and Southern Africa (with the exception of the Kalahari desert; Figure 4.8a,e). Functional richness was also moderately high in central continental Palaearctic in the breeding season (Figure 4.8a), but this was much reduced in the non-breeding season (Figure 4.8e,i). Functional evenness was very low across Western Africa in the breeding season (Figure 4.8c), but increased in this region in the non-breeding season (Figure 4.8g,k).

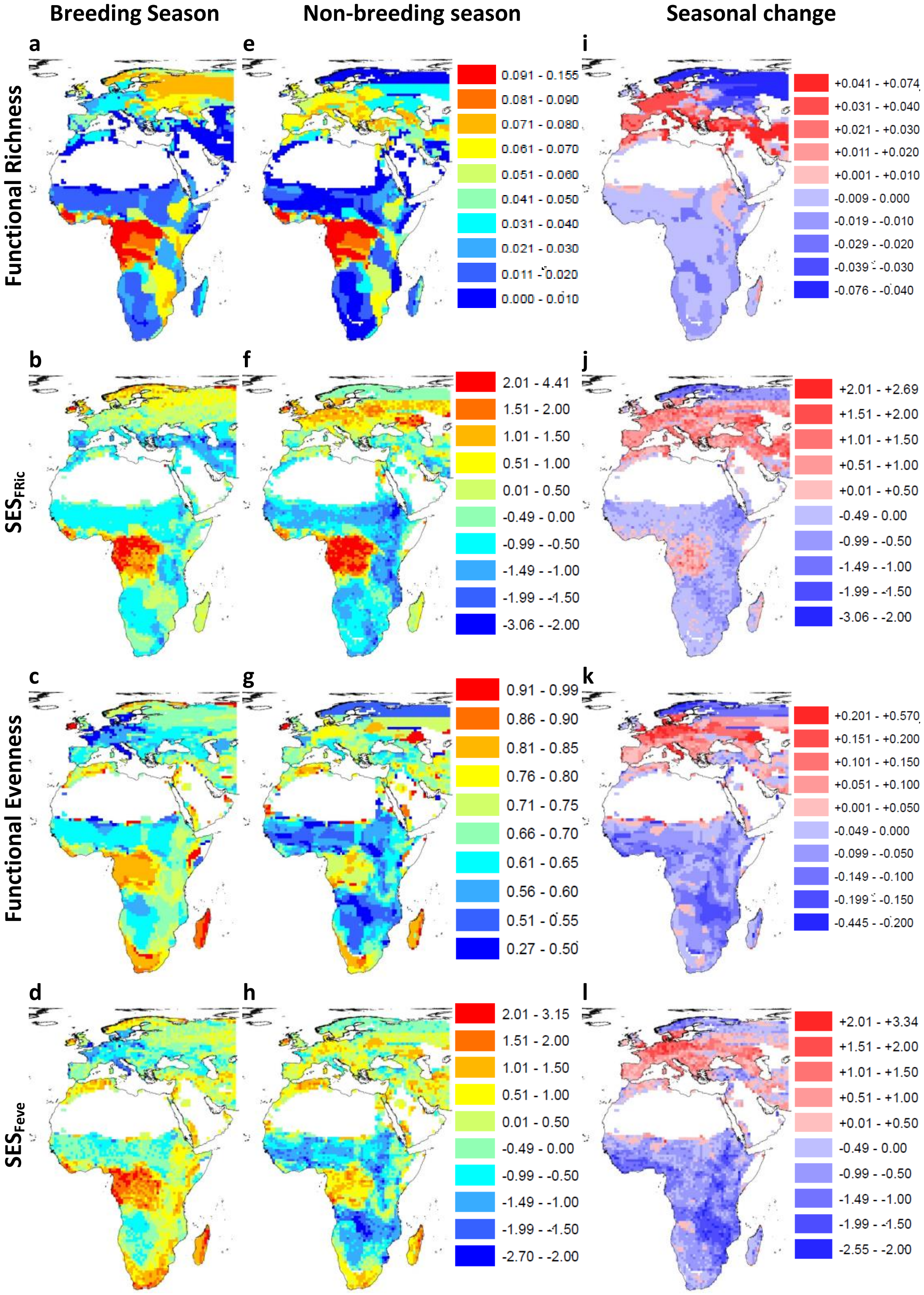

Figure 4.5: The functional richness (FRic) (a & e), Standardised Effect Size of functional richness (SES_{Fric}) calculated using a null model to take account of species richness (b & f), functional evenness (FEve) (c & g) and Standardised Effect Size of functional evenness (SES_{Feve}) (d & h) of assemblages of terrestrial predators during the breeding season (a-d) and non-breeding season (e-h) and the change in (i) FRic, (j) FEve, (k) SES_{Fric}, (l) SES_{Feve} (non-breeding season minus breeding season). Functional richness measures the volume of functional space occupied and functional evenness measures the regularity of species in functional spaces; see Figure 4.1.

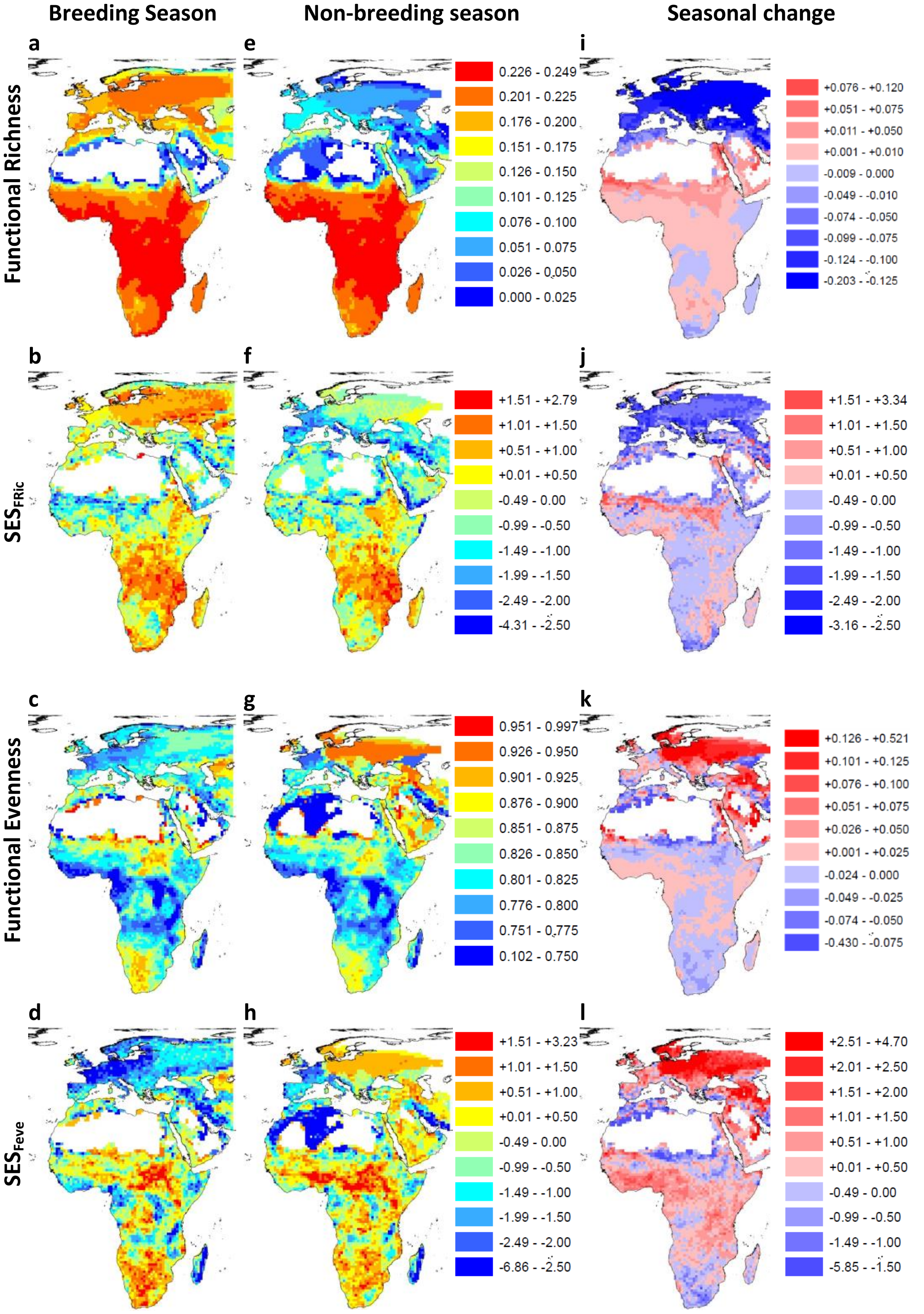

Figure 4.6: The functional richness (FRic) (a & e), Standardised Effect Size of functional richness (SES$_{Fric}$) calculated using a null model to take account of species richness (b & f), functional evenness (FEve) (c & g) and Standardised Effect Size of functional evenness (SES$_{Feve}$) (d & h) of assemblages of terrestrial insectivores during the breeding season (a-d) and non-breeding season (e-h) and the change in (i) FRic, (j) FEve, (k) SES$_{Fric}$, (l) SES$_{Feve}$ (non-breeding season minus breeding season). Functional richness measures the volume of functional space occupied and functional evenness measures the regularity of species in functional spaces; see Figure 4.1.

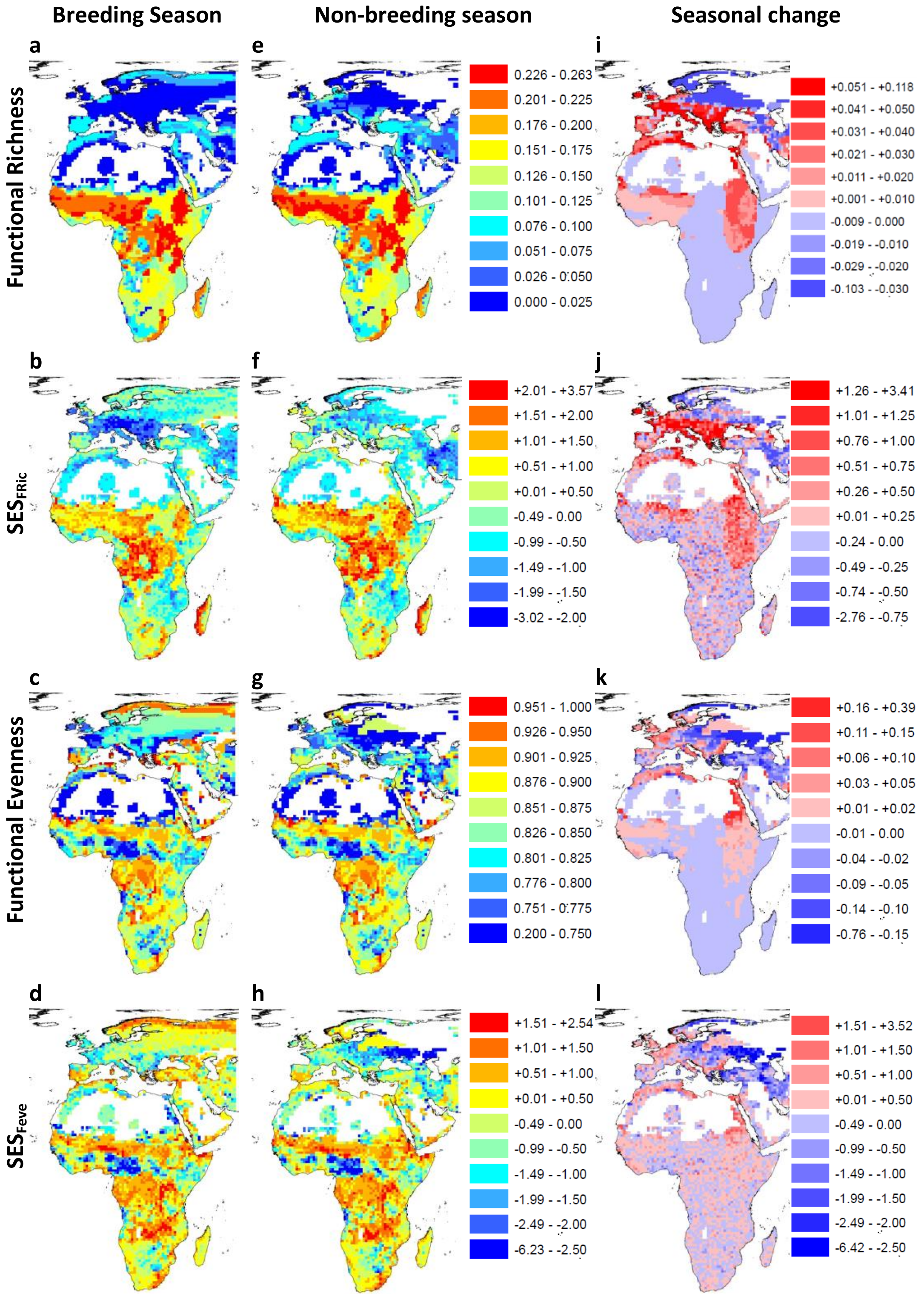

Figure 4.7: The functional richness (FRic) (a & e), Standardised Effect Size of functional richness (SES$_{Fric}$) calculated using a null model to take account of species richness (b & f), functional evenness (FEve) (c & g) and Standardised Effect Size of functional evenness (SES$_{Feve}$) (d & h) of assemblages of terrestrial herbivores during the breeding season (a-d) and non-breeding season (e-h) and the change in (i) FRic, (j) FEve, (k) SES$_{Fric}$, (l) SES$_{Feve}$ (non-breeding season minus breeding season). Functional richness measures the volume of functional space occupied and functional evenness measures the regularity of species in functional spaces; see Figure 4.1.

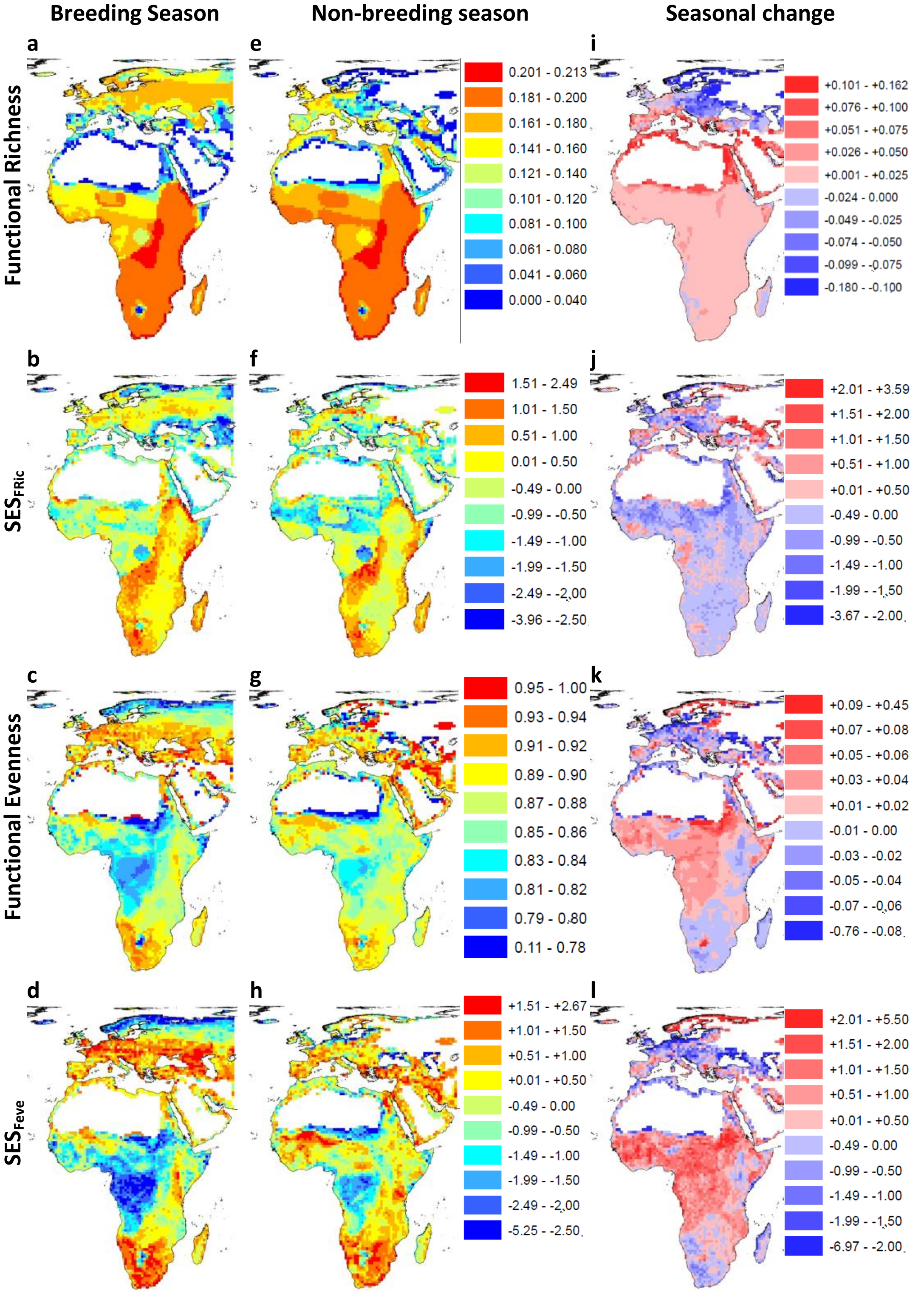

Figure 4.8: The functional richness (FRic) (a & e), Standardised Effect Size of functional richness (SES_{Fric}) calculated using a null model to take account of species richness (b & f), functional evenness (FEve) (c & g) and Standardised Effect Size of functional evenness (SES_{Feve}) (d & h) of assemblages of aquatic foragers during the breeding season (a-d) and non-breeding season (e-h) and the change in (i) FRic, (j) FEve, (k) SES_{Fric}, (l) SES_{Feve} (non-breeding season minus breeding season). Functional richness measures the volume of functional space occupied and functional evenness measures the regularity of species in functional spaces; see Figure 4.1.

Taxonomic dissimilarity was highest at the northernmost latitudes and was relatively low across most of the Afrotropics (Figure 4.9a,d). The proportion of taxonomic dissimilarity that is attributable to nestedness was higher than that attributable to species turnover, except at approximately 30°N-50°N, where there was high species turnover (Figure 4.9). Functional dissimilarity was high in the north continental Palaearctic and in arid regions (Sahara desert and Arabian Peninsular) and low or zero across most of the Afrotropics (Figure 4.10a,d), i.e. large areas showed no difference in the functional space occupied in each season. Functional dissimilarity was lower than taxonomic dissimilarity in most cells (Supplementary Figure 7) and was mainly attributable to functional nestedness, i.e. winter functional space is a subset of summer functional space in the higher latitudes and vice versa in the tropical latitudes (Figure 4.10) There was very low functional turnover in the great majority of grid cells, although the average functional turnover was highest around 35°N (Figure 4.10). Taking the functional richness and functional dissimilarity results together, it suggests that there was very little change in the functional space occupied in each season in the Afrotropics (i.e. the functional space occupied in each season has very high or complete overlap), but the distribution of species in that space must be changed by the high number of migratory species in their wintering grounds (Figure 4.3).

Overall, resident and migratory species occupied similar parts of the functional space (Figure 4.11). The resident species of the Afrotropics were well-distributed across functional space (Figure 4.11a), whereas residents of the Palaearctic were more restricted to high values of the first dimension (Figure 4.11b). The distribution of the resident species of the Afrotropics was similar to the distribution of another set of tropical resident species, those of IndoMalaya (Figure 4.11c). The overall distribution of migratory species in functional space showed more similarities to the Palaearctic residents' distribution (Figure 4.11d) as they also showed greater occupancy at higher values of the first dimension (except Afrotropic-Palaearctic migrants, which were distributed around a centroid value of 0 on the first dimension and none of these species had high values (>0.25) on this dimension).

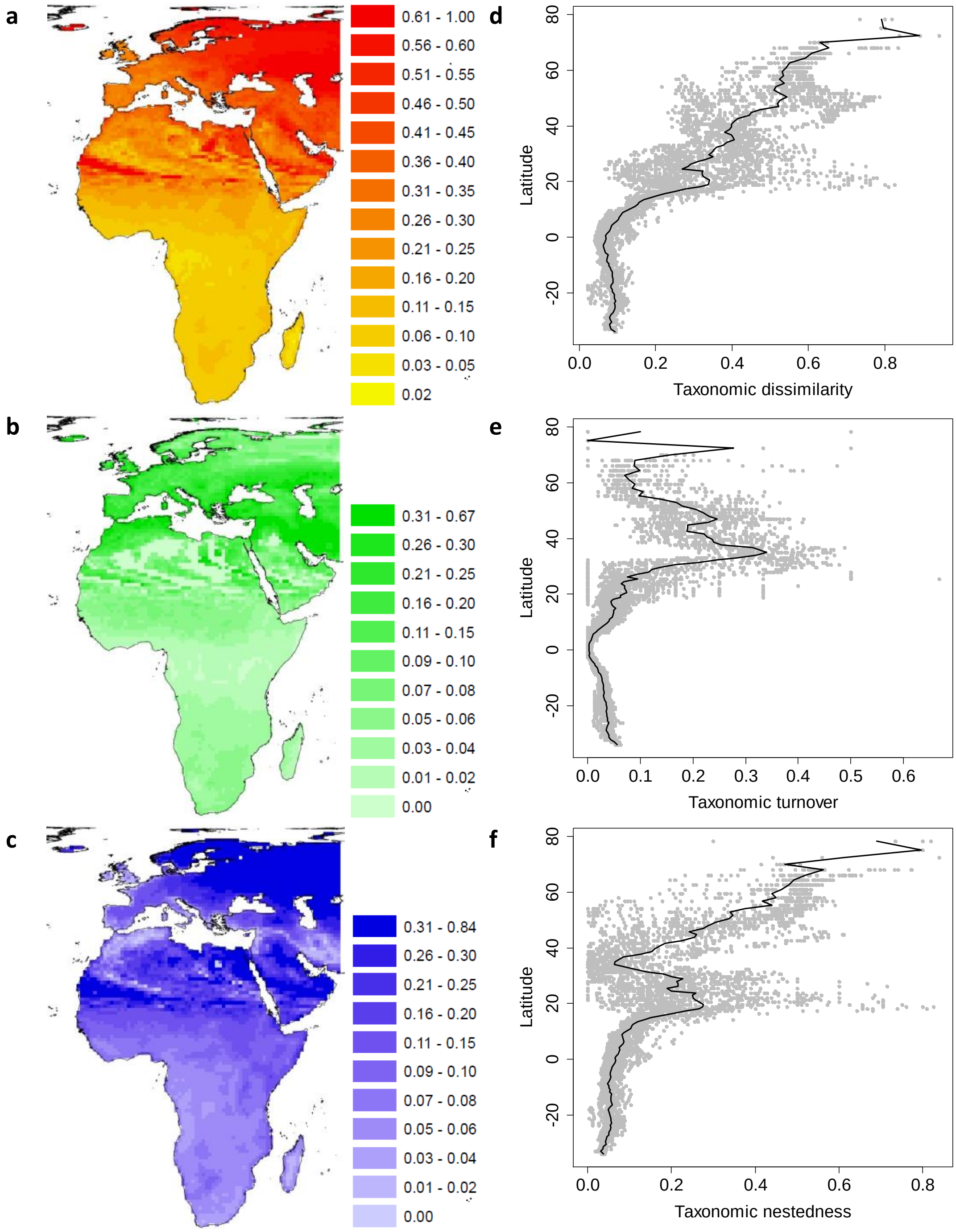

Figure 4.9: The taxonomic dissimilarity (proportion of species not shared by two communities) of cells in the breeding and non-breeding seasons: (a) the change in community composition between seasons; (b) the change in community composition that is attributable to species turnover; (c) the change in community composition that is attributable to nestedness. (d-f) The latitudinal distribution of taxonomic dissimilarity. Grey symbols show cell values and black lines show latitudinal averages.

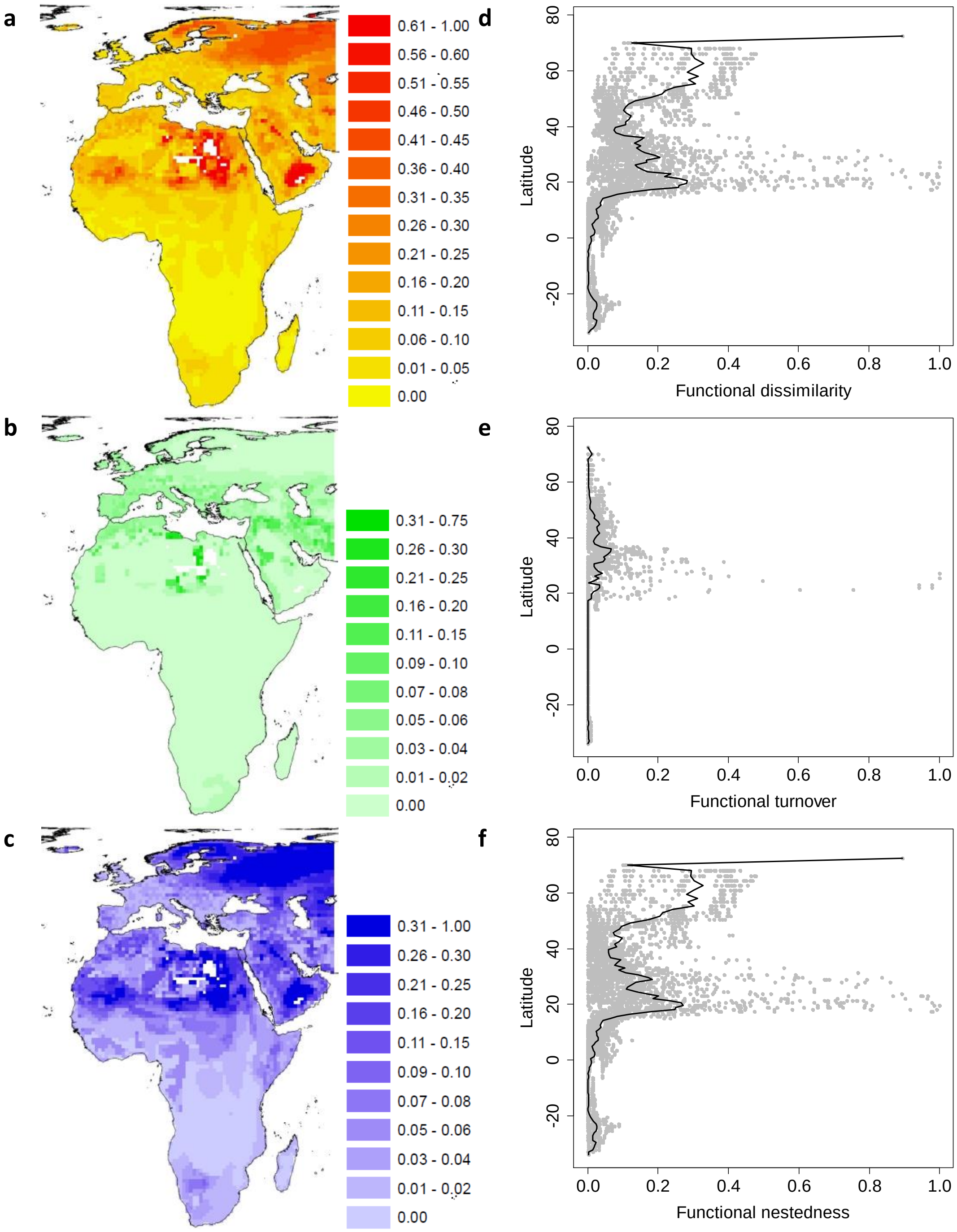

Figure 4.10: The functional dissimilarity dissimilarity (proportion of the functional space of two communities that does not overlap) of cells in the breeding and non-breeding seasons: (a) the change in functional trait space occupied between seasons; (b) the change in functional trait space occupied that is attributable to species turnover; (c) the change in functional trait space occupied that is attributable to nestedness. (d-f) The latitudinal distribution of functional dissimilarity. Grey symbols show cell values and black lines show latitudinal averages.

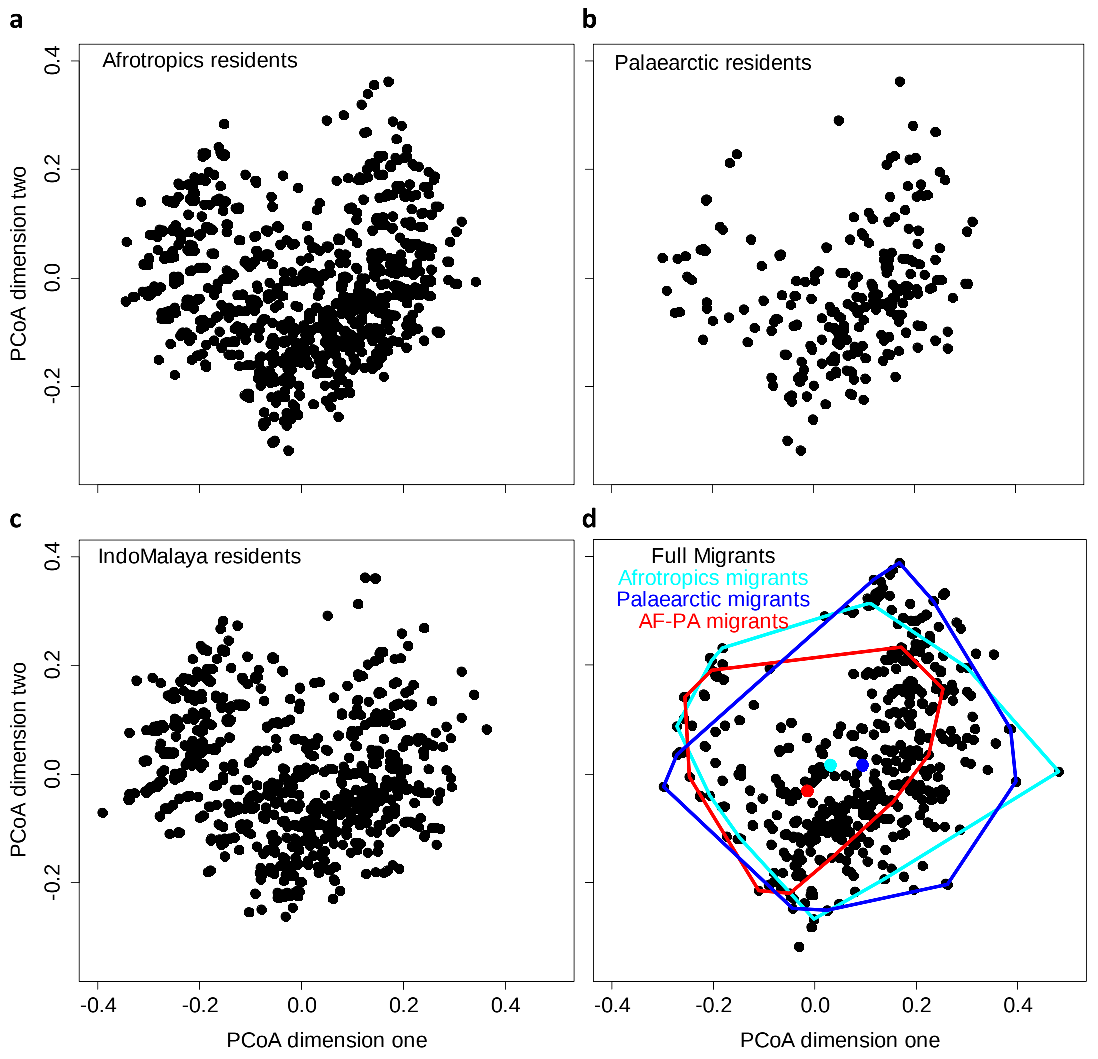

Figure 4.11: The distribution of bird species in functional trait space using PCoA dimensions one and two for (a) non-migratory species in the Afrotropics, (b) non-migratory species in the western Palaearctic, (c) non-migratory species in IndoMalaya and (d) full migrants in the Afrotropics and western Palaearctic. The convex hull and centroids are shown for migratory species with breeding and non-breeding ranges in the Afrotropics, migratory species with breeding and non-breeding ranges in the Palaearctic and migratory species with breeding ranges in the Palaearctic and non-breeding ranges in the Afrotropics.

4.5 Discussion

There is considerable change in bird community composition in the Afrotropics and the Western Palaearctic as a result of migration. At high latitudes more than 70% of the species present in some cells in the breeding season were not present in the non-breeding season (Figure 4.3a). This is consistent with a recent analysis of migratory birds across the globe, which found a transition zone between approximately 30°N and 40°N where species richness is approximately equal in both seasons and north of which species richness is substantially higher in the summer months (Somveille *et al.*, 2013). However, in most cells the taxonomic dissimilarity between seasons was greater than the functional dissimilarity (Figure 4.9a; Figure 4.10a; Supplementary Figure 7). This suggests that the effects on ecosystem processes as a result of the change in species composition may be moderated by different species having similar roles so that the seasonal change in the occupation of functional space is smaller than would be suggested by the change in community composition. This is corroborated by the finding that migrants and residents occupied similar parts of the functional space (Figure 4.11) and that there is a saturating relationship between species richness and functional richness (Supplementary Figure 4); i.e. there is functional redundancy in cells with high species richness.

The emigration of species from the high latitudes of the Palaearctic corresponded with a decrease in the volume of functional space occupied during the winter months (Figure 4.4a,e,i). These areas largely corresponded with northern areas where functional richness was lower than expected by chance, as indicated by the negative values of SES_{FRic} (Figure 4.4f). The high functional dissimilarity of cells between the breeding and non-breeding seasons in this area was a result of the functional space occupied in the non-breeding season being nested within the functional space occupied in the breeding season, i.e. there was very little functional turnover (Figure 4.10). This suggests that the combination of species present during the non-breeding season is a result of the harsh climatic conditions restricting the range of trait combinations that permit survival – i.e. environmental filtering. Analysis of the traits of non-breeding waders in UK estuaries has shown that community assembly is consistent with environmental filtering (Mendez *et al.*, 2012) and extreme temperatures and low precipitation are predictors of low functional richness of fish assemblages across Europe (Schleuter *et al.*, 2012).

Environmental filtering might manifest itself differently for each of the functional groups. For example, functional richness of terrestrial insectivores is very low during the non-breeding season in the Palaearctic since there is very low availability of flying insect prey (Figure 4.6). The northern range limits of winter distributions of insectivorous bird species in North America were found to be warmer than predicted from physiological limits, suggesting that they are not found further north because of food limitation rather than because of an inability to maintain body temperature (Canterbury, 2002). Functional richness of terrestrial predators was also much lower during the non-breeding season as species that rely on small mammals and other prey that may be seasonally unavailable due to hibernation or snow cover migrate south, e.g. Hen Harrier (*Circus cyaneus*) and Northern Long-eared Owl (*Asio otus*). Other predators may be following migrating prey, e.g. Marsh Harriers (*Circus aeruginosus*) prey upon aquatic birds and passerines (Del Hoyo *et al.*, 1994) that may themselves be migratory. Predators that do remain at high latitudes year-round are capable of hunting available prey, for example by targeting vertebrates that are present year-round such as grouse (e.g. Northern goshawk *Accipiter gentilis*, Del Hoyo et al., 1994) or by being able to locate prey under snow cover (e.g. Boreal owl *Aegolius funereus*, Del Hoyo et al., 1999). In some parts of the northern Palaearctic there were too few aquatic foragers to calculate functional diversity for this functional group during the non-breeding season (Figure 4.8) as ice freeze-up sees their foraging habitat disappear during winter. Species richness of this group was much lower in the non-breeding season at high latitudes and globally above 45°N the proportion of waterfowl species present in the non-breeding season that are migratory is mostly 100% (Dalby *et al.*, 2014). Indeed, the freezing over of foraging habitats can be the trigger for migratory birds to leave their breeding grounds, as with the Whooper Swans (*Cygnus cygnus*) of Chuna Lake in Russia whose departure dates are highly correlated with the date the lake freezes each year (Gilyazov & Sparks, 2002). Additionally, the winter abundance of dabbling ducks (*Anas* spp.) in Missouri can be explained by an index of weather severity incorporating temperature, cumulative freezing days and snow depth and duration (Schummer *et al.*, 2010).

In comparison, functional richness was relatively high across the Afrotropics in both seasons (Figure 4.4a,e) and there was only a small increase in the non-breeding season (Figure 4.4i), despite the high numbers of migratory species present during this season (Figure 4.3c). It is thought that high species richness can result from finer niche partitioning (Hutchinson, 1959), which enables high species packing. The small change in functional richness of the Afrotropics in the non-breeding season may also be a reflection of finer niche partitioning; species can specialise on a narrow range of resources when those resources are in plentiful supply so more species can occupy the overall functional space volume (i.e. greater species packing). The arrival of migratory species in the Afrotropics during the winter months did little to change the overall volume of functional space utilised. Instead, there were changes in the distribution of species within that space.

Functional evenness was low across most of the Afrotropics, particularly in the Eastern Arc and the Congo basin (Figure 4.4c,g) and functional evenness was lower in the non-breeding season than the breeding season, indicating that species were more clustered in functional space (Figure 4.4k). This is consistent with the suggestion that there is finer niche partitioning in the non-breeding season and therefore species are more similar to one another. Analyses based on breeding ranges have shown that tropical bird assemblages have more specialised diet and habitat niches than temperate assemblages (Belmaker *et al.*, 2012). However, different functional groups show different patterns. For example, birds that forage exclusively in/on water, of which nearly two-thirds of the species in these analyses are migratory (Table 4.2), increase the functional evenness of the majority of the cells in the Afrotropics in which they are present during the non-breeding season (Figure 4.8). This indicates that they may be occupying part of the functional space that is relatively underused by resident species and therefore there is more regularity in species' positions in functional space during the non-breeding season than the breeding season, as with Scolopacidae wintering in west Africa (Moreau, 1972). As previously discussed, plentiful resources enable high species packing since species can specialise on a narrow range of resources. In contrast, when resources are scare, species may need to be more generalist, with wider niche breadths, and this therefore permits only low species packing (and high functional evenness). This can be seen in the distribution of insectivores in continental Palaearctic in the non-breeding season; there is increased functional evenness compared to the breeding season (Figure 4.6k). Residents in this region are adapted to survive seasonality of climate and of resource availability, which can drive increased niche breadth (Evans *et al.*, 2005).

Analogous to the species richness transition zone identified by Somveille *et al.* (2013), there is a region between approximately 30°N and 50°N, which show some interesting inter-seasonal patterns in functional diversity. This region has high species turnover between seasons (Figure 4.9b,e), but lower functional dissimilarity than either of the regions immediately north or south (Figure 4.10a,d). Compared to other parts of the Palaearctic, it has low functional nestedness (Figure 4.10c,f), but does show some evidence of functional turnover (Figure 4.10b,e). Therefore species that breed in this region and winter further south may be replaced in the non-breeding season by species that breed at higher latitudes, but which are functionally similar to the departing species. For example, the Booted Eagle (*Hieraatus pennatus*) breeds in Southern Europe and winters further south and it hunts small vertebrate prey, much like the Merlin (*Falco columbianus*) and Hen Harrier, which breed at high latitudes and winter in Southern Europe (Del Hoyo *et al.*, 1994).

The analyses presented here indicate that the distribution of functional diversity is substantially different in the breeding and non-breeding seasons and that migratory species make important contributions to functional diversity in their breeding and wintering areas. For example, the migratory species that breed in the higher latitudes of the Palaearctic considerably increase the volume of functional space occupied. Since functional traits and the use of functional trait space are thought to affect ecosystem processes (Cadotte *et al.*, 2011; Mason *et al.*, 2005), migratory species might be providing important ecosystem services to which resident species cannot contribute so effectively because they do not share the same traits. Reduction of arthropods in tropical agroforestry systems was found to correlate with migratory bird species richness, but not resident species richness; therefore migratory bird species are reducing plant damage by reducing pest populations (Van Bael *et al.*, 2008). Moreover, migratory species can provide links for ecosystem services that cover great distances. For example, waterfowl can provide long distance dispersal between wetlands for both plant seeds and aquatic invertebrate eggs (Figuerola *et al.*, 2003). However, many migratory species are globally threatened, near-threatened or declining; European breeding birds that winter in Africa have shown stronger population declines compared with resident and short-distance migrants (Sanderson *et al.*, 2006). Therefore these ecosystem services could themselves be under threat. Future changes in migratory patterns are expected as a result of climate and land use change and are already manifesting themselves as changes in community composition in Europe (Lemoine *et al.*, 2007). Climate change may put long-distance migrants at a competitive disadvantage compared to short-distance migrants and resident species (Sanderson *et al.*, 2006; Lemoine & Böhning-Gaese, 2003). In these analyses, there was very low functional diversity of aquatic foragers in the non-breeding season at northern latitudes (Figure 4.8). However, water birds are shifting their wintering distributions northwards in response to climate change (Lehikoinen *et al.*, 2013; Maclean *et al.*, 2008) and this will affect the distribution of functional diversity of this group.

It has been suggested that identifying areas of high functional diversity could be a way of setting conservation priorities in order to maintain ecosystem processes and services (Devictor *et al.*, 2010). These analyses have shown that for taxa whose distributions change considerably between seasons, using breeding distributions will not identify all the most important areas for biodiversity conservation. For example, eastern Egypt has higher functional richness in the non-breeding season than the breeding season (Figure 4.4a,e,i) and there is a high proportion of its species that are only present in the non-breeding season (Figure 4.3c,d). Indeed, the majority of Egypt's bird species are non-breeding migrants that use the country for passage or wintering, especially soaring birds and water birds (Baha El Din, 2001). From another perspective, functional relationships between species could be used to identify which groups of species would be most important to conserve in terms of maintaining ecological function (Walker, 1992). However, a particular guild may have lower functional redundancy in their wintering grounds than their breeding grounds (and vice versa), so they may meet the criteria for prioritising their conservation only in a particular season. Therefore, migratory species need to be conserved even in sites where they show high redundancy as they may be more functionally important elsewhere and as a result require protection across their annual range.

4.6 Conclusions

The annual movement of billions of birds between their breeding and wintering grounds causes changes in the taxonomic and functional composition of communities than can affect ecosystem processes. In northerly regions, functional diversity is much lower in the non-breeding season compared to the breeding season, reflecting environmental filtering restricting the species and their respective traits that can remain resident during the winter months. Species that use these areas as their breeding grounds increase the functional diversity during the breeding season and may therefore be contributing to ecosystem processes (e.g. pest control and seed dispersal) that would not be so effective or efficient in their absence. Despite the huge numbers of birds using the Afrotropics as their wintering grounds, they make a relatively small contribution to the overall functional space occupied. This, coupled with the decrease in functional evenness during the non-breeding season, suggests that there is increased niche partitioning during the time when they join resident populations. Since migratory birds make important contributions to functional diversity in their breeding and wintering grounds, this is another reason to prioritise their conservation. When using biodiversity hotspots to identify important areas for conservation, different seasonal distributions must be considered for migratory taxa.

Chapter Five: The role of intrinsic and extrinsic factors in predicting the sensitivity to habitat disturbance of species at local scales and their global extinction risk: a study of birds in South and South-East Asia

5.1 Abstract

Aim: Species are threatened by extrinsic factors such as habitat disturbance, high human population density, agricultural expansion and urbanisation. Their sensitivity to these factors may in part be determined by intrinsic factors such as their biological traits. The aim of this chapter is to compare the relative importance of intrinsic and extrinsic factors in predicting the sensitivity of bird species to habitat disturbance at a local scale and their global extinction risk.

Location: South and South-East Asia

Methods: Mixed models were used to identify the intrinsic and extrinsic factors associated with (a) absence from disturbed habitats based on local-scale bird surveys and (b) higher extinction risk based on IUCN Red List status. To account for phylogenetic effects, family was included as a random effect. All combinations of models were ranked using AIC and the sum of Akaike weights for each predictor was used to evaluate its relative importance.

Results: At the local scale, all the intrinsic factors together explained less variance ($r^2 = 0.067$) than the single extrinsic factor, disturbance ($r^2 = 0.187$), whereas the intrinsic factors explained a greater proportion of the variance in global extinction risk ($r^2 = 0.214$) than the extrinsic factors ($r^2 = 0.134$). Species were more sensitive at both local and large scales if they were highly forest dependent and/or had a narrow habitat breadth, but the importance of other traits was scale-dependent.

Main conclusions: The importance of intrinsic factors in determining sensitivity to habitat disturbance was more evident at large than local scales. Species of least conservation concern may become threatened in the future if they have intrinsic traits that render them sensitive to local-scale disturbance and inhabit regions that are set to experience increasing habitat disturbance.

Key words: Agriculture, extinction, forest dependency, habitat breadth, habitat loss, Red List, traits, urbanisation

5.2 Introduction

Biodiversity is currently being lost at rates far higher than natural extinction rates (Barnosky *et al.*, 2011). Of around 10,000 bird species, 134 have gone extinct since 1500, 1313 (13.0%) are threatened with extinction and a further 880 (8.7%) are near-threatened (IUCN, 2013). Habitat loss and degradation are the greatest threats for birds; 93% of threatened species are impacted through processes such as the expansion of agriculture, logging and deforestation (Birdlife International, 2008). It is estimated that the total number of birds across the globe has declined by between a fifth and a quarter since pre-agricultural times as a result of land-use changes (Gaston *et al.*, 2003). Furthermore, Gaston and Spicer (2004) speculate that since the arrival of anatomically modern humans, their activities may have driven half of all recent bird species extinct. Species are more likely to be threatened with extinction if they inhabit areas where these threatening processes (extrinsic factors) are more intensive, such as regions of high human population density (e.g. Mckinney, 2001). Other extrinsic factors could include habitat loss through processes such as urbanisation or agricultural expansion. However, the ability of species to withstand threatening extrinsic factors may in part be a consequence of intrinsic factors such as their biological traits.

Threatened and near-threatened birds are not randomly distributed with regard to their biological traits; for example frugivores and scavengers are more likely to be extinction-prone than members of other guilds (Şekercioğlu *et al.*, 2004). This could have important consequences for ecosystem services, for example frugivores may be important seed dispersers. Additionally, increased specialisation, such as narrow diet or habitat breadth, is associated with a higher risk of extinction; farmland specialists are showing steeper population declines than habitat generalists because the latter are buffered against the effects of agricultural intensification due to their flexibility in being able to use other habitat types (Pocock, 2011). Overall, generalist species may be more persistent than specialist species as they can be more adaptable in the face of environmental change (Sodhi *et al.*, 2005b). Habitat modification may also have differential effects on species according to where they forage; for example, Peh *et al.* (2005) found that species that forage on the ground were particularly vulnerable to the effects of logging, whereas species that foraged on tree trunks could persist in human-modified landscapes. Some species regularly use manmade sites for feeding, e.g. rubbish dumps, agricultural land; these species could therefore be expected to persist in disturbed habitats.

Several authors have found a relationship between body size and extinction risk (e.g. Owens & Bennett, 2000; Sodhi *et al.*, 2004b; Peh *et al.*, 2005; Gaston & Blackburn, 1995), with possible explanations including these species being present at lower densities or requiring greater habitat or diet resources. A species' life history traits may affect its ability to cope with threatening processes. K-selected species with a long generation length and a high investment in a smaller number of offspring may be less resilient in the face of increased adult mortality (e.g. Webb *et al.*, 2002). Contrastingly, short-lived species have potentially high rates of increase to allow them to recover from threatening processes. Additionally, altricial young could be predicted to be more vulnerable than precocial young while they remain in the nest, since an entire brood is more likely to be lost than a single chick.

Geographically restricted or endemic species have been found to be more susceptible to extinction (e.g. Posa & Sodhi, 2006; Waltert *et al.*, 2004) and geographic range size is one of the criteria used for classifying species on the Red List (IUCN, 2013). Restricted altitudinal range has been shown to be associated with extinction risk (Lee *et al.*, 2005), which may be indicative of species being unable to avoid disturbance by elevational migration due to physiological intolerance. Migratory status may also affect sensitivity; European breeding birds that winter in Africa have shown stronger population declines compared with resident and short-distance migrants (Sanderson *et al.*, 2006). Understanding what makes some species more prone to extinction than others could guide conservation efforts to reduce species loss, but it is necessary to consider the importance of both intrinsic and extrinsic factors (Blackburn & Gaston, 2002; Tingley *et al.*, 2013).

This study concerns the avifauna of South and South-east Asia; one of the world's richest regions in terms of biodiversity, but also one of the most threatened. This area holds five of Myers *et al.*'s (2000) biodiversity hotspots, characterised by high levels of both endemism and habitat loss: Indo-Burma, Western Ghats and Sri Lanka, Philippines, Sundaland and Wallacea. Each of these hotspots contains between 1500 and 15000 endemic plant species and between 355 and 701 endemic vertebrate species, but they have lost 85-97% of their primary vegetation (Myers *et al.*, 2000). Currently 44% of the species which have been assessed in this region have a decreasing population trend (IUCN, 2013). It has been estimated that up to 42% of South-east Asia's species will be extinct by the end of the century with at least half of those being endemic species, which will therefore be globally extinct (Brook *et al.*, 2003). Sodhi et al. (2004a) identified a number of threats to biodiversity in this region, with deforestation and logging being the most destructive. A recent review on the same topic concluded that conversion of logged and primary forest to plantations, especially oil palm, is an even more pressing issue (Wilcove *et al.*, 2013). Globally, threatened birds occur in all habitat types, but three-quarters are found in forest, particularly in tropical areas (Birdlife International, 2012). Indonesia and the Phillipines have been identified as being of especially high conservation importance globally, since the impact of forest loss in these areas would mean significant losses to global avian biodiversity because of the richness of forest-dependent birds (Buchanan *et al.*, 2011).

In this chapter, we identify the importance of extrinsic and intrinsic factors in determining extinction risk in south and south-east Asian birds. The conclusions drawn on the relative importance of different factors affecting extinction risk could in part depend on the scale at which the study is conducted. The factors that correlate with global extinction risk may well be different from those that are associated with local population declines or extirpations (Collen *et al.*, 2011). Therefore, this study is conducted at two different scales with two different response variables. Firstly, local biodiversity surveys in disturbed habitats (compared to primary habitat) will be used to identify species that have become locally extinct and those more resilient species that remain in the disturbed area. Then the IUCN Red Lists status of all bird species across the region will be used to identify factors associated with global extinction risk.

5.3 Methods

5.3.1 Local responses to habitat disturbance

South and South-East Asia is defined in this study as comprising the biogeographic realm of IndoMalaya and the Wallacea region (Figure 5.1). Literature searches and expert knowledge were used to identify publications that compared avian biodiversity in disturbed and undisturbed habitats in this region. The 34 publications identified recorded the presence/absence or abundance (which was converted to presence/absence) of bird species in an undisturbed forest habitat and at least one disturbed habitat. These publications are summarised in Table 5.1 and their locations are shown in Figure 5.1. There are records for 645 species from 70 families (excluding species that were only found in the disturbed habitat).

Table 5.1: The sources of data used for the occurrence of species in disturbed and undisturbed habitats. The number of records in a given source may be greater than the number of species where there were multiple records for one species in different disturbed habitats, e.g. the same species was surveyed in logged forest and a plantation.

Source	**Location**	**Type(s) of disturbance**	**Number of species**	**Total records**
Adeney *et al.* (2006)	Bukit Barisan Selatan National Park, Sumatra	Burning	106	106
Anggraini *et al.* (2000)	Bukit Barisan Selatan National Park, Sumatra	Burning Disturbance	4	8
Ansell *et al.* (2011)	Yayasan Sabah logging concession, Malaysian Borneo	Logging	79	79
Aratrakorn *et al.* (2006)	Krabi Province, Thailand	Plantation	101	101
Chettri *et al.* (2001)	Yuksam–Dzongri trekking corridor, India	Disturbance	79	79
Cleary *et al.* (2007)	Kayu Mas concession, Kalimantan	Logging	144	144
Danielsen & Heegaard (1995)	Riau & Jambi, Sumatra	Plantation	64	64
Das & Deori (2010)	Nameri National Park, India	Disturbance Secondary	124	248
Edwards *et al.* (2011)	Yayasan Sabah logging concession, Malaysian Borneo	Logging	150	150
Jepson & Djarwadi (1999)	Jambi, Sumatra	Plantation	40	40
Johns (1986)	Sungai Tekam Forestry Concession, Malaysia	Logging	179	179
Lambert (1992)	Ulu Segama Forest Reserve, Sabah, Malaysia	Logging	64	64
Lammertink (2004)	Kutai & Gunung Palung National Parks, Kalimantan	Logging	14	14
Marsden (1998)	Seram, Indonesia	Logging	15	15
Peh *et al.* (2005)	Johore, Malaysia	Rural Secondary	156	312
Phalan *et al.* (2011)	Udham Singh Nagar district, India	Agriculture Plantation	100	100
Posa & Sodhi (2006)	Subic Bay, Philippines	Logging Rural Suburban Urban	41	163
Round *et al.* (2006)	Khao Luang, southern Thailand	Disturbance Plantation	80	160
Shahabuddin & Kumar (2007)	Sariska Tiger Reserve, India	Disturbance	47	47
Shankar Raman & Sukumar (2002)	Kalakad-Mundathurai Tiger Reserve, India	Logging Secondary	47	94
Sheldon *et al.* (2010)	Kalabakan Forest Reserve, Sabah, Malaysia	Plantation	162	162
Sheldon & Styring (2011)	Sarawak Planted Forest Project, Sarawak	Logging Plantation	66	132
Sidhu *et al.* (2010)	Thattekad and Anamalai Hills, India	Plantation Rural	106	212
Slik & Van Balen (2006)	Balikpapan, Kalimantan	Burning	149	149
Sodhi *et al.* (2005a)	Lore Lindu National Park, Sulawesi	Plantation Rural Secondary	29	85
Styring & Ickes (2001)	Pasoh Forest Reserve, Malaysia	Logging	15	15
Styring & Bin Hussin (2004)	Sungai Lalang Forest Reserve, Malaysia	Logging	13	13
Thiollay (1995)	Bukit Barisan Selatan & Mount Kerinc NPs & Maninjau, Sumatra	Plantation	177	177
Velho *et al.* (2012)	Pakke Wildlife Sanctuary and Tiger Reserve, western Arunachal Pradesh, India	Logging	29	29
Waltert *et al.* (2004)	Lore Lindu National Park, Sulawesi	Agroforestry Secondary	17	34
Waltert *et al.* (2005)	Lore Lindu National Park, Sulawesi	Agroforestry Logging	11	22
Wijesinghe & Brooke (2005)	Sinharaja rain forest, Sri Lanka	Logging Plantation	27	54
Wilson & Johns (1982)	South of the Mahakam River, Kalimantan	Logging Plantation	4	8
Zakaria *et al.* (2005)	Sungai Lalang Forest Reserve, Malaysia	Logging	16	16
		TOTAL	645	3375

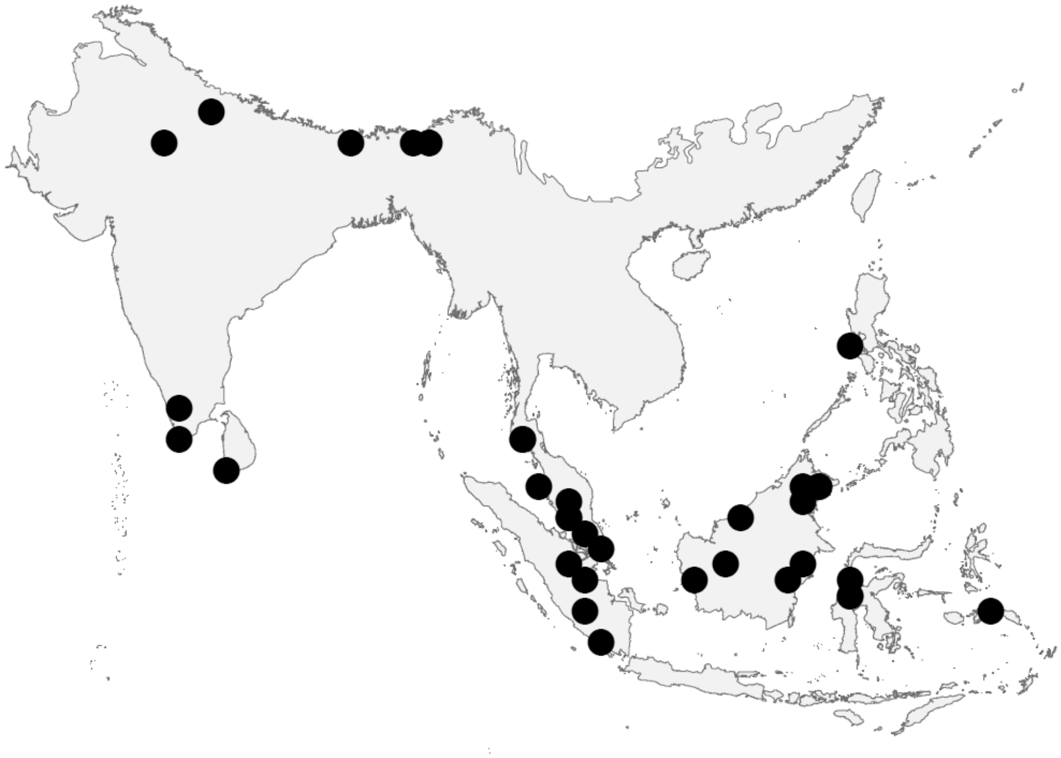

Figure 5.1: A map of South and South-East Asia showing the locations of the studies which form the sources of data used for the occurrence of species in disturbed and undisturbed habitats.

5.3.2 Global extinction risk

Shape-files of species' ranges were provided by BirdLife International (Birdlife International & Natureserve, 2011). These polygon maps are based on known locations (e.g. geo-referenced point locality records, collecting locality of museum specimens) and expert opinion (see Buchanan *et al.* (2011) for details). For each species, the areas in which it is considered extant or probably extant through the year or only in the breeding season were included and areas where it was considered possibly extant or possibly extinct or where its presence was uncertain were excluded. Using these criteria, the range maps of 2004 bird species were found to overlap with the study region. Of these, 8 species were classified as "Data Deficient" by IUCN and were therefore excluded from the analysis. Of the remaining 1996 species, 28 (1.4%) were classified as "Critically Endangered" (CR), 40 (2.0%) were "Endangered" (EN), 133 (6.7%) were "Vulnerable" (VU), 248 (12.4%) were "Near-Threatened" (NT) and 1547 (77.5%) were "Least Concern" (LC).

By overlaying each species range map with a grid using the Behrmann cylindrical equal-area projection (cell resolution 96.486 km x 96.486 km, equivalent to a 1° longitude and 1° latitude grid at the 30° latitude of true scale) with associated data on human population density and the proportion of land areas with agricultural or urban landuse (Klein Goldewijk *et al.*, 2011), we were able to calculate an area-weighted mean value for human population density (1.31-2288.92 persons km^{-2}), the proportion of land area with human population density >10.km^{-2} (0.02-1.00) and proportion of land area under agricultural (0.05-0.91) and urban (<0.01-0.09) landuse.

5.3.3 Biological and ecological traits

We tested the effects of species' traits that have previously been hypothesised or demonstrated to be associated with sensitivity to disturbance by other authors (as outlined in the introduction), and are summarised in Table 5.2. These were largely different traits than those used to calculate functional diversity in previous chapters. The traits associated with functional diversity were purported to be 'functional effect traits', which affect ecosystem function (Hooper *et al.*, 2005). In contrast, the traits associated with sensitivity to disturbance are 'functional response traits' since they determine how species respond to environmental disturbance (Hooper *et al.*, 2005). Some traits may be considered as both functional effect traits and functional response traits. For example, body weight is a functional effect trait when considering resource use since it determines the amount of resources consumed. Body weight is also a functional response trait since large body size has been found to be associated with higher extinction risk (e.g. Owens & Bennett, 2000; Sodhi *et al.*, 2004b; Peh *et al.*, 2005; Gaston & Blackburn, 1995), which could be due to lower density of populations or greater resource requirements.

Although geographic range size has been found to be a strong predictor of extinction risk (Lee & Jetz, 2011), we did not include it in the models as species can be classified for the Red List on the basis of their range size (criteria B1); for example species may be classified as endangered if their extent of occurrence is less than 5000km^2. Trait values for each species were collated using a variety of sources (listed in Appendix S1: Sources used for bird trait data). Where data were not available for individual species (<7% of species-trait combinations), genus, or failing that family, values were used (Table 5.2). Overall, 93.8% of the species-trait combinations used were specific to individual species, 6.0% were genus averages and 0.2% were family averages.

Table 5.2: The biological and ecological traits used in the full generalised linear mixed model (GLMM) to test associations with sensitivity to human disturbance and extinction risk. Where possible, data were collated for individual species. Missing values were filled with genus or, failing that, family values.

Trait	Values	Data specificity		
		Species	Genus	Family
Altitudinal range / $\log_e$(m)	3.40 – 8.41	93.4%	5.9%	0.7%
Diet breadth (total number of different diet items recorded)	1 – 12	93.1%	6.9%	-
Development at hatching	0 (altricial) 1 (semialtricial) 2 (precocial)	87.8%	12.2%	-
Diet type	Carnivore Frugivore Herbivore Insectivore Omnivore	93.4%	6.6%	-
Forest dependency	0 (does not usually use forest) 1 (low) 2 (medium) 3 (high)	100.0%	-	-
Foraging location	Aerial Ground Vegetation Water General (>1 of the above)	93.3%	6.7%	-
Generation length	2.4 – 19.8	100.0%	-	-
Habitat breath (total number of different habitat types used)	1 – 28	100.0%	-	-
Manmade site use (e.g. feed on crops, in gardens, at feeding stations, rubbish tips, manmade ponds or reservoirs, etc.)	0 (not known) 1 (rare/infrequent) 2 (frequent)	87.7%	12.3%	-
Movement	Migrant Nomad Partial migrant/nomad Regular elevational movements Resident/sedentary	100.0%	-	-
Weight / $\log_e$(g)	1.63 – 8.03	83.1%	15.2%	1.7%

5.3.4 Statistical analysis

All statistical analysis was carried out using R version 2.12.0 (R Development Core Team, 2010). The local-scale data regarding species presence in disturbed habitats were used to create a binary response variable: 1 = present in both the disturbed and undisturbed habitats and 0 = absent from the disturbed habitat. This response variable was modelled in a Generalised Linear Mixed Model (GLMM) with fixed effects including the biological traits (intrinsic factors) in Table 5.2 and the type of disturbance (extrinsic factor). The random effects included the identity of the study from which the data were taken in order to account of a range of study- and site-specific effects, such as recorder effort, and of non-independence of response within studies. Some species were recorded in more than one study and some were recorded in disturbed habitats in one study and only in the undisturbed habitat in another. To account for this, each record was treated as a separate data point and species was nested within the random effect of study. The family to which the species belonged was also included as a random effect in order to account for niche conservatism and the effects of phylogeny. As a measure of the variance explained by the model, pseudo-R^2 was calculated using the function *r.squaredGLMM* in the MuMIn package (Barton, 2013). The output from this function includes the marginal R^2 (the variance explained by the fixed factors) and the conditional R^2 (the variance explained by both fixed and random factors).

To identify the intrinsic and extrinsic factors associated with global extinction risk, we used a linear mixed model (LMM) with Red List status as the response variable (converted to a numerical scale; 1=LC to 5=CR) and fixed factors of biological traits (intrinsic factors) and human population density and human landuse (extrinsic factors). Family was included as a random factor in order to account for niche conservatism and the effects of phylogeny.

For both the local-scale and large-scale models, species weight and altitudinal range were $\log_e$-transformed to reduce skew and proportional variables were logit-transformed. Variance inflation factors (VIF) were calculated, which were each <<10 (Quinn & Keough, 2002), indicating that model predictors were not strongly inter-correlated. All possible combination of each model were fitted using the *dredge* function in the MuMIn package (Barton, 2013). Models were ranked by AIC to identify the best supported models. Using the 95% confidence set of models (i.e. those in which the cumulative Akaike weights of the models in rank order of AIC was ≤0.95), model-averaging was used to calculate parameter estimates (Burnham & Anderson, 2002). For each factor, the summed Akaike weights of the models in which they were included were used to assess their relative importance (Burnham & Anderson, 2002).

Since geographic range size has been found to be a strong predictor of extinction risk (Lee & Jetz, 2011), an additional analysis was performed using the global extinction risk of range-restricted species (those with the 25% smallest ranges; 499 species). Geographic range size was calculated in ArcMap 10.0 (ESRI, 2010) in square kilometres. We also separately analysed the predictors of global extinction risk for those species which were most highly exposed to human activity – those species that were in the highest 10% of species for the average human population density across their range or for the proportion of their range with >10people.km^{-2}, with agricultural land cover or urban land cover (487 species, of which 210 were also range-restricted species).

The model-averaged parameter values for intrinsic factors from the local-scale model were used to predict the relative extirpation risk for all 1,996 species across the region. Linear regression analysis was used to assess the level of congruence between the predicted relative extirpation risk and the global threat status of species. The predicted risk values for each species were also used to calculate the average sensitivity for each grid cell across South and South-East Asia. We also used these values to identify those species that are currently of Least Concern globally, which have a higher predicted sensitivity locally (lowest 25% of scores of all LC species).

5.4 Results

Species that were listed as globally threatened or near threatened were more likely to also also be recorded as being sensitive at the local scale (always absent from the disturbed habitat in all studies in which they were recorded) than being resilient at the local scale (always present in both the disturbed and undisturbed habitats in all papers in which they were recorded). Of the four endangered species, all were also locally sensitive, while 86% of the vulnerable species and 60% of the near-threatened species were also locally sensitive (Figure 5.2). However, species that were globally of least concern were more likely to be locally resilient (69%; Figure 5.2).

At the local scale, all the intrinsic factors together explained less variance than the single extrinsic factor, type of disturbance (6.7% and 18.8%, respectively, Table 5.3). When all possible combinations of models were compared, the most important variables in explaining local extirpation were the type of disturbance, whether a species was migratory, its habitat breadth, its dependence on forest habitats, its development at hatching and its use of manmade sites (Table 5.3).

Species were most likely to be sensitive to urban areas, whereas they were least sensitive to burning, secondary forest and logging (Table 5.4). Species were more likely to be absent from the disturbed habitat if they were full or partial migrants or nomads and more likely to be present in the disturbed habitat if they were sedentary or if they were altitudinal migrants. Species were more likely to be absent from the disturbed habitat if they had a narrow habitat breadth, were highly dependent on forest habitats or were not known to use manmade sites for feeding. They were also more likely to be absent from the disturbed habitat if they had precocial young.

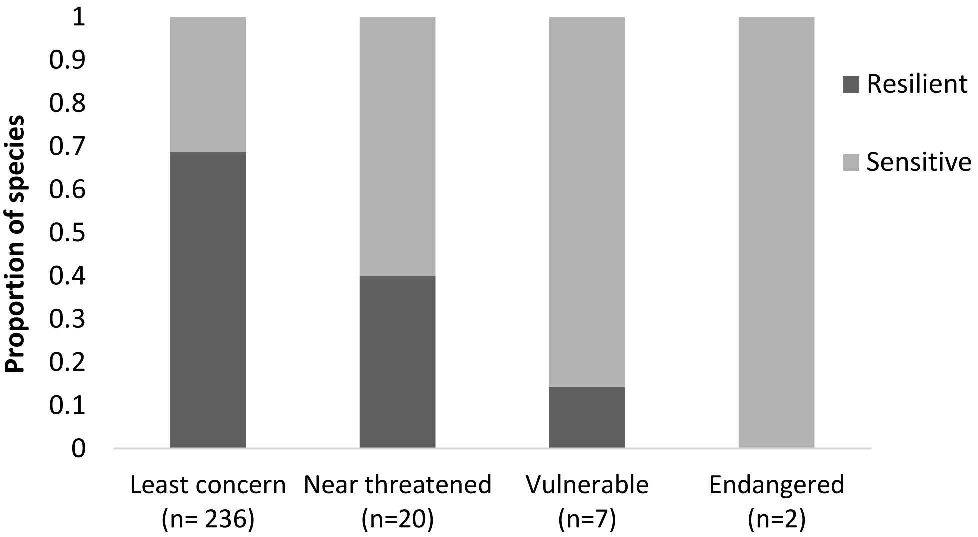

Figure 5.2: The proportion of species in different threat categories that are listed as either 'resilient' (species which were present in the disturbed habitat in all the papers in which they were recorded) or 'sensitive' (species which were absent from the disturbed habitat in all the papers in which they were recorded). There was a significant association between local sensitivity and global threat status (χ^2=18.36, df=3, p=0.0004).

Table 5.3: The variance explained by intrinsic factors (traits) and extrinsic factors (human disturbance) in different model subsets. Each factor was tested individually, as well as all intrinsic factors together and all extrinsic factors together. Variance explained is measured as pseudo-R^2.

	Marginal r^2 (Variance explained by fixed factors)			
		Global extinction risk		
Model predictors	Local extirpation	All species	Range-restricted species	Highly vulnerable species
All intrinsic factors (traits)	0.067	0.214	0.235	0.169
Altitudinal range	0.000	0.052	0.036	0.019
Development at hatching	0.015	0.015	0.042	0.006
Diet breadth	0.005	0.014	0.000	0.012
Diet type	0.003	0.009	0.002	0.022
Foraging location	0.003	0.002	0.029	0.004
Forest dependency	0.017	0.053	0.001	0.073
Generation length	0.010	0.014	0.012	0.003
Habitat breadth	0.020	0.049	0.013	0.045
Manmade site use	0.018	0.019	0.000	0.019
Movement	0.002	0.028	0.021	0.033
Weight	0.009	0.081	0.152	0.028
All extrinsic factors[1]	0.187	0.134	0.134	0.128
Human population density	-	0.009	0.014	0.052
Proportion of range: >10 people.km^{-2}	-	0.120	0.040	0.116
Proportion of range: agriculture	-	0.000	0.060	0.000
Proportion of range: urban	-	0.002	0.001	0.020

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[1] For the local extirpation model, the only extrinsic factor was the type of disturbance (see Table 5.1).

Table 5.4: The model-averaged parameter estimates for the 95% confidence model set predicting (i) local extirpation (positive parameter values indicate greater probability of being present in the disturbed habitat, i.e. resilient; see Supplementary Table 8), and (ii) global threat status for all species (see Supplementary Table 9), endemic species and highly exposed species (positive parameter values indicate greater global threat status). [a] Zero by default, i.e. intercept.

Variable	**Parameter estimates**			
		Global extinction risk		
	Local extirpation	All species	Range-restricted species	Highly vulnerable species
Altitudinal range	-0.16 (±0.12) NS	-0.17 (±0.02)****	-0.32 (±0.07)****	-0.11 (±0.05)*
Development at Hatching	-0.73 (±0.18)****	+0.07 (±0.04) NS	+0.09 (±0.09) NS	+0.10 (±0.08) NS
Diet Breadth	+0.10 (±0.04)**	-0.03 (±0.01)*	-0.02 (±0.04) NS	-0.09 (±0.03)**
Diet Type: carnivore	0[a]	0[a]	0[a]	0[a]
: frugivore	-0.13 (±0.35) NS	+0.13 (±0.12) NS	-0.17 (±0.27) NS	+0.36 (±0.26) NS
: herbivore	+0.25 (±0.37) NS	+0.20 (±0.10)*	+0.24 (±0.25) NS	+0.18 (±0.21) NS
: insectivore	+0.26 (±0.26) NS	+0.25 (±0.07)***	+0.22 (±0.20) NS	+0.15 (±0.17) NS
: omnivore	+0.32 (±0.24) NS	+0.10 (±0.07) NS	-0.08 (±0.19) NS	-0.02 (±0.15) NS
Forest dependency	-0.37 (±0.09)****	+0.11 (±0.02)****	-0.03 (±0.06) NS	+0.17 (±0.04)***
Foraging location: aerial	0[a]	0[a]	0[a]	0[a]
: general	-0.08 (±0.21) NS	+0.10 (±0.07) NS	-0.11 (±0.25) NS	-0.02 (±0.18) NS
: ground	-0.38 (±0.27) NS	+0.04 (±0.08) NS	-0.30 (±0.26) NS	-0.11 (±0.190) NS
: vegetation	-0.14 (±0.21) NS	-0.00 (±0.08) NS	-0.33 (±0.25) NS	-0.16 (±0.18) NS
: water	-1.41 (±0.61)*	-0.06 (±0.11) NS	-0.33 (±0.45) NS	+0.02 (±0.28) NS
Generation length	-0.05 (±0.03) NS	+0.01 (±0.01) NS	+0.01 (±0.02) NS	-0.01 (±0.02) NS
Habitat breadth	+0.09 (±0.02)****	-0.01 (±0.00)**	-0.06 (±0.03) NS	-0.01 (±0.01) NS
Manmade Site Use	+0.24 (±0.07)**	-0.01 (±0.02) NS	-0.05 (±0.09) NS	-0.02 (±0.05) NS
Movement: migrant	0[a]	0[a]	0[a]	0[a]
: nomad	+0.53 (±0.35) NS	+0.14 (±0.11) NS	-0.39 (±0.46) NS	+0.10 (±0.27) NS
: partial migrant/nomad	-0.21 (±0.29) NS	+0.01 (±0.07) NS	-0.31 (±0.46) NS	-0.03 (±0.19) NS
: regular elevational movements	+0.66 (±0.32)*	-0.14 (±0.08) NS	-1.07 (±0.42)*	-0.31 (±0.21) NS
: resident/sedentary	+0.87 (±0.24)***	-0.02 (±0.06) NS	-0.76 (±0.36)*	-0.09 (±0.16) NS
Weight	-0.13 (±0.07) NS	+0.19 (±0.02)****	+0.34 (±0.05)****	+0.17 (±0.04)****
Disturbance: Agriculture	0[a]	-	-	-
: Agroforestry	-0.20 (±0.74) NS	-	-	-
: Burning	+2.81 (±1.03)**	-	-	-
: Disturbance	-0.02 (±0.41) NS	-	-	-
: Logged	+2.03 (±0.40)****	-	-	-
: Plantation	+0.31 (±0.31) NS	-	-	-
: Rural	-0.13 (±0.38) NS	-	-	-
: Secondary Forest	+2.90 (±0.40)****	-	-	-
: Suburban	+0.48 (±0.56) NS	-	-	-
: Urban	-2.81 (±0.82)***	-	-	-
Human Population density	-	-0.03 (±0.03) NS	-0.06 (±0.07) NS	+0.03 (±0.04) NS
Proportion range >10 people.km^{-2}	-	+0.09 (±0.01)****	+0.07 (±0.01)****	+0.08 (±0.01)****
Proportion range agriculture	-	+0.17 (±0.06)**	+1.04 (±0.16)****	+0.68 (±0.19)***
Proportion range urban	-	-0.17 (±0.05)***	-0.53 (±0.10)****	+0.01 (±0.11) NS

At the global scale, the intrinsic factors explained a greater proportion of the variance in extinction risk ($r^2 = 0.214$) than the extrinsic factors ($r^2 = 0.134$; Table 5.3). In terms of intrinsic factors, species were more likely to be globally threatened if they were large-bodied, had a small altitudinal range, were dependent on forest and had a narrow habitat or diet breadth. Insectivores and herbivores were more likely to be threatened than carnivores, frugivores or omnivores (Table 5.4). Of the extrinsic factors considered, species were more likely to be threatened if a large proportion of their range had a high human population density (>10 people.km^{-2}) or if a large proportion was covered by agricultural land. Conversely, they were less likely to be threatened if a high proportion of their range was urban.

Intrinsic factors also explained a greater proportion of the variance in global extinction risk for range-restricted species ($r^2 = 0.235$) than did extrinsic factors ($r^2 = 0.134$; Table 5.3). As with the complete model of species across the region, range-restricted species were more likely to be globally threatened if they were large-bodied and had a small altitudinal range (Table 5.4). They were also more likely to be threatened if they were full or partial migrants or nomads than if they were sedentary species or elevational migrants. Unlike the full model, there were no significant effects of forest dependency, habitat breadth or diet type. As with all species, range-restricted species were more likely to be threatened if a large proportion of their range had a high human population density or if a large proportion was covered by agricultural land, but were less likely to be threatened if a high proportion of their range was urban.

Intrinsic factors explained a smaller proportion of the variance in global extinction risk for highly exposed species ($r^2 = 0.169$), but it was still greater than the variance explained by extrinsic factors ($r^2 = 0.128$; Table 5.3). Highly exposed species were also more likely to be threatened if they were large-bodied, highly dependent on forest, had a narrow diet breadth or a small altitudinal range (Table 5.4). As with all species and range-restricted species, highly exposed species were more likely to be threatened if a large proportion of their range had a high human population density or if a large proportion was covered by agricultural land, but there was no effect of the proportion of their range that was urban.

Regression analysis showed there was a significant relationship between the predicted relative extirpation risk (calculated using the 95% confidence model average) and Red List status (Figure 5.3).

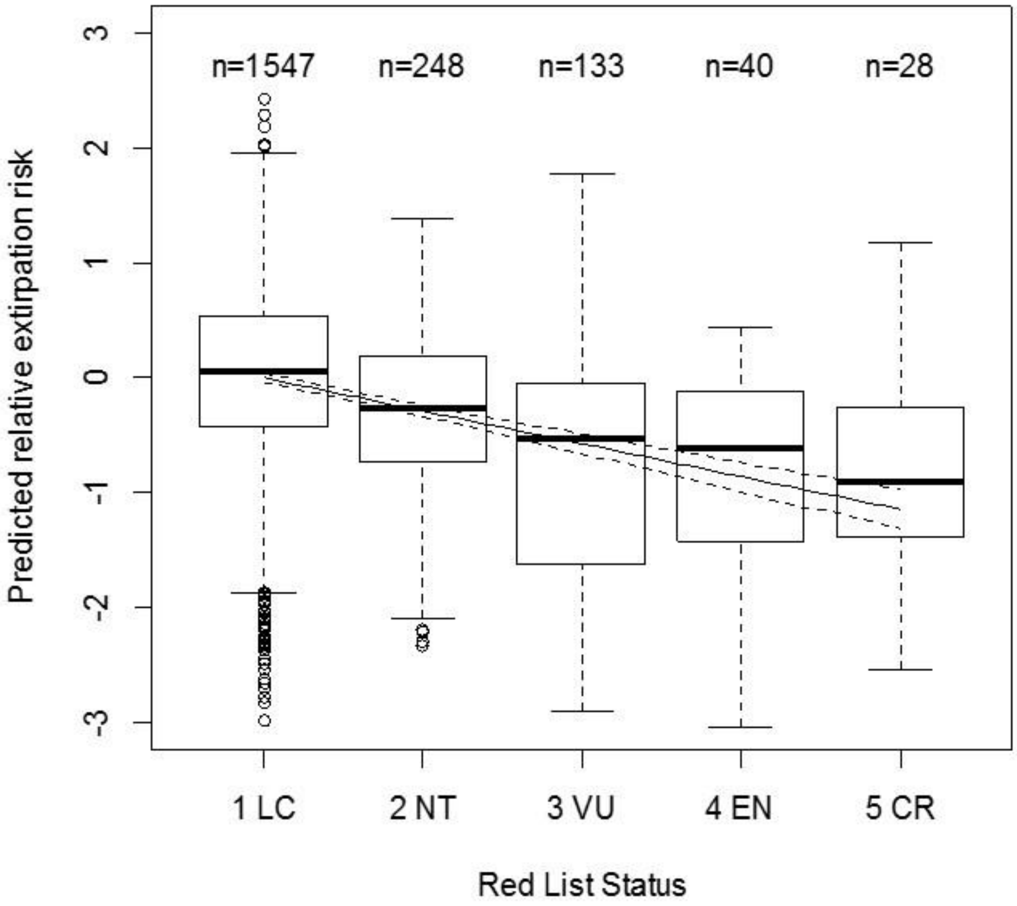

Figure 5.3: The relationship between the predicted relative extirpation risk using the 95% confidence model average (low values indicate greater sensitivity) and red list status (Linear regression: $y = 0.279 - 0.351x$, $F_{1,1994} = 159.6$, $r^2 = 0.074$, $p < 0.0001$). Regression line and 95% confidence intervals (dashed lines) are shown. Relative extirpation risk was modelled using presence in (1) or absence from (0) disturbed habitats in local studies (given that all species considered were found in an undisturbed habitat in each study). Positive values therefore indicate that species were more likely to be present in the disturbed habitat, i.e. were more resilient to disturbance. The averaged model is summarised in Table 5.4.

In order to identify whether traits that were found to be more important in predicting sensitivity at the local scale were also important in predicting global threat status, the importance of traits at each scale were plotted against each other (Figure 5.4a) as measured by Akaike weights summed across all models including each trait. At both local and large scales, habitat breadth and forest dependency were among the most important traits that predicted sensitivity (Figure 5.4a). Body weight, altitudinal range and diet type appear to be more important at large scales than local scales, whereas generation length, development at hatching and use of manmade sites were more important at the local scale (Figure 5.4a).

The most important traits for predicting global threat status may vary when just range-restricted or highly exposed species are considered. Therefore, the importance of traits in predicting global threat status for all species in South and South-east Asia were plotted against the importance of traits for range-restricted species (Figure 5.4b) and against the importance of traits for highly exposed species (Figure 5.4c). The most important traits for predicting global threat status for all species in South and South-East Asia (weight and altitudinal range) were also the most important traits for predicting threat status of range-restricted species (Figure 5.4b). However, some other traits such as forest dependency were much less important for range-restricted species alone. There was reasonable correspondence between the importance of some of the traits for all species and highly exposed species (Figure 5.4c). Diet type, movement, foraging location, habitat breadth and development at hatching were less important for highly exposed species.

The average predicted sensitivity (using the 95% confidence model of local extirpation) was high in Borneo, Sulawesi, the Philippines and Sumatra (Figure 5.5a) – where threatened and near-threatened species also made up a relatively high proportion of the total species (Figure 5.5b) – and low in India. The areas with the highest proportion of species predicted to be locally sensitive (lowest quartile of predicted sensitivity using the local scale model, see Figure 5.3 and list in Supplementary Table 10), but recorded as being Least Concern were Southern China, Western India and Sulawesi and the areas with the lowest proportion of these species were Borneo, Sumatra and southern Thailand (Figure 5.5c).

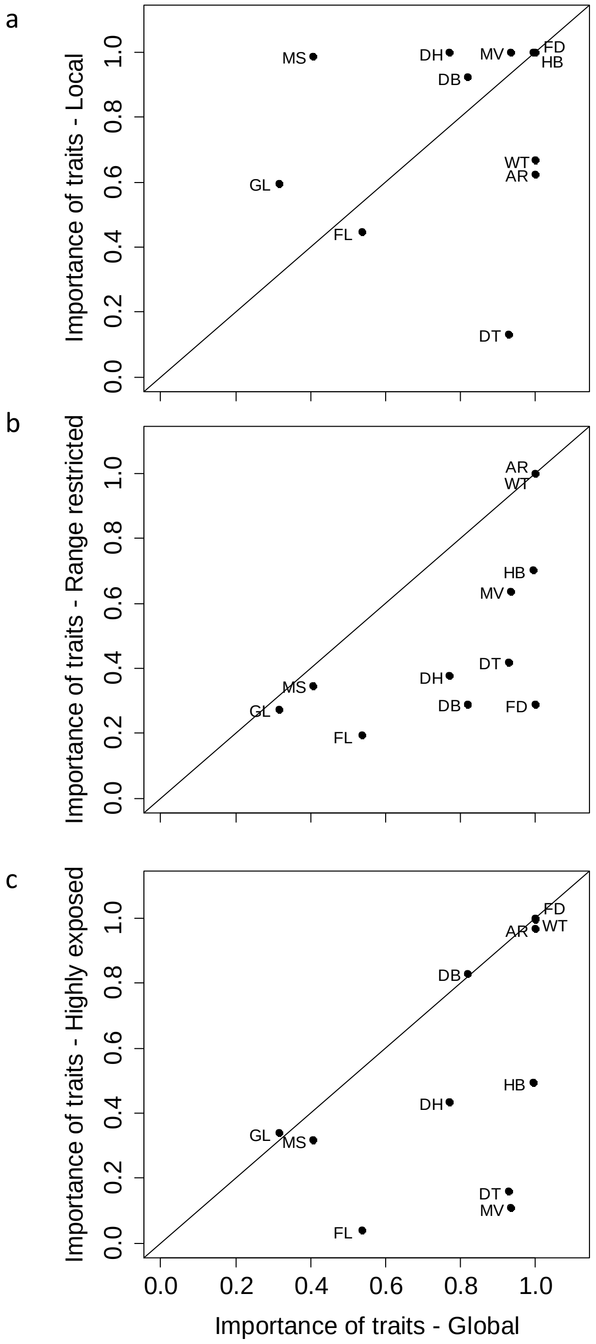

Figure 5.4: The importance of traits (as measured by Akaike weights summed across all models including each trait) for predicted global threat status for all species in South and South-East Asia compared to (a) sensitivity to local disturbance (r = 0.094, p = 0.784) (b) global threat status for range-restricted species in the region (r = 0.617, p = 0.043), and (c) global threat status for highly exposed species in the region (r = 0.506, p = 0.112). Straight line indicates 1:1 correspondence. AR = Altitudinal range, DB = Diet breadth, DH = Development at hatching, DT = Diet type, FD = Forest dependency, FL = Foraging location, GL = Generation length, HB = Habitat breadth, MS = Manmade site use, MV = Movement, WT = Weight.

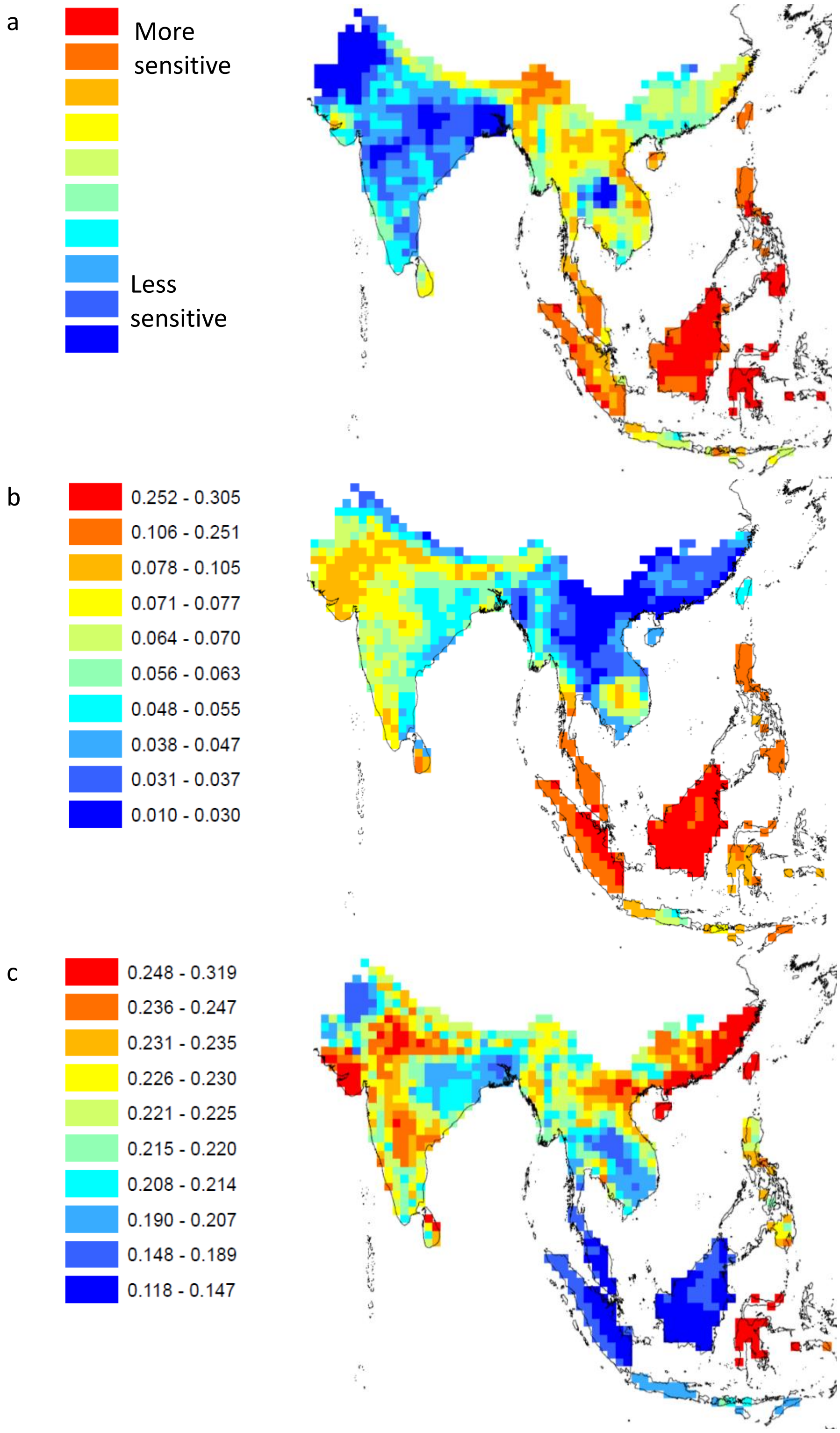

Figure 5.5: The distribution of (a) mean predicted sensitivity using the 95% confidence model of traits of species surveyed in disturbed and undisturbed habitats, (b) proportion of species threatened or near-threatened, and (c) proportion of species predicted locally sensitive, but globally of Least Concern (lowest quartile of predicted sensitivity for LC species using the local scale model, see Figure 5.3). Predicted sensitivity was calculated using the model-averaged parameters for all traits (Table 5.4).

5.5 Discussion

Species that were sensitive to disturbance at local scales were also more likely to be globally threatened (Figure 5.2) and there was a weak but significant relationship between the predicted sensitivity from the local-scale model and global threat status (Figure 5.3). However, there were differences in the factors that were associated with local and global sensitivity. At the local scale, the type of disturbance to which a species was subjected was more important than its biological traits in determining its sensitivity to disturbance (Table 5.3) and species were most sensitive to urbanisation compared to other threatening processes (Table 5.4). Urban areas are one of the most rapidly increasing land uses; more than half of the world's population live in urban areas and the population increase of 2.3 billion people by 2050 is expected to mainly be absorbed by urban areas (UN, 2012). Approximately 8% of terrestrial vertebrates on the Red List are threatened primarily because of urbanisation (Mcdonald *et al.*, 2008). Birds with certain traits are more successful at colonising and surviving in urban environments, primarily generalists, herbivores and above-ground nesting species (Evans *et al.*, 2011). The detrimental effects of urbanisation on biodiversity could in part be mediated by urban planning; compact rather than sprawling urban design enables more green spaces to provide habitat fragments (Sushinsky *et al.*, 2013), i.e. land sparing rather than land sharing *sensu* Green *et al.* (2005), and additional resources could be provided to increase biodiversity such as supplemental food and nesting sites for ground-nesting birds (Evans *et al.*, 2011). Species were least sensitive to burning, logging and secondary forest (Table 5.4). In one of the studies used for the local-scale analysis in this chapter, Slik & Van Balen (2006) found that although species remained even in twice-burned forest, they occurred at much lower densities. Therefore, analyses of abundance change rather than extirpation may yield quite different results. Logging is thought to be very damaging to biodiversity, but a comparison of unlogged with logged forest in South-east Asia found that more than three-quarters of bird species found in unlogged forest were also found in twice-logged forest, including threatened species (Edwards *et al.*, 2011). There could be a time lag between the logging, or other human disturbances, and the biodiversity response; extinctions can occur generations after the disturbance and therefore communities experience an extinction debt (Tilman *et al.*, 1994). Wearn *et al*. (2012) demonstrated that historical deforestation in the Amazon has created a considerable extinction debt; 80% of the extinctions as a result of deforestation in this area are yet to come.

Intrinsic factors explained a relatively small proportion of the variance in local-scale responses to habitat disturbance (Table 5.3). This is consistent with Collen *et al.* (2011) who found that intrinsic biological variables had lower explanatory power for population decline of mammals compared to extrinsic environmental variables (in single predictor models head-body length explained 1% of the variance in total population change, compared to mean potential evapotranspiration and temperature across the range which explained 3% and 4% respectively). One reason that traits explain only a small proportion of the variance in local response to habitat disturbance could be that these sites are experiencing an extinction debt (Tilman *et al.*, 1994); some of the species that were found to be present in the disturbed habitat might therefore be expected to go locally extinct in the future. Migratory behaviour was the most important trait for local-scale responses to disturbance and full or partial migrants or nomads were more likely to be absent from the disturbed habitat than sedentary species or elevational migrants (Table 5.4). There are two ways in which this can be interpreted. Firstly, it could indicate that migratory species are more vulnerable to disturbance than sedentary species. This is consistent with other studies that have found that migrants are more sensitive (Sanderson *et al.*, 2006). Alternatively, it could indicate behavioural flexibility on the part of migratory species; sedentary species are less likely to disperse from disturbed habitats to more favourable sites. Specialists were less likely to persist in the disturbed habitat; narrow habitat and/or diet breadth and high forest dependency were associated with greater sensitivity, whereas species that are known to use manmade sites such as crops, gardens and feeding stations were more likely to be present in disturbed habitats (Table 5.4). Generalists are thought to be more resilient than specialists as they can be more flexible and adaptable to changing environmental conditions (e.g. Sodhi et al., 2005b; Pocock, 2011). It has been shown that forest loss in this region would have a high impact on the global biodiversity of forest-dependent species (Buchanan et al., 2011). Species that produced precocial young were also more sensitive to disturbance (Table 5.4). Lee & Jetz (2011) found that precocial birds had higher extinction risk and suggested that this could be due to young being more vulnerable to human-introduced nest predators since they lack parental protection.

At large scales, intrinsic factors were more important than extrinsic factors in determining extinction risk (Table 5.3). Species were more likely to be threatened with extinction if they were large-bodied (Table 5.4). Large-bodied species have been found to be more sensitive to human persecution and predation by introduced species since they are more sensitive to adult mortality as a result of their slow life histories (Owens & Bennett, 2000). Additionally, large-bodied species have on average smaller population sizes, require larger areas of habitat and more food, have greater habitat specificity and feed at higher trophic levels, all of which make them more vulnerable to disturbance (Gaston & Blackburn, 1995; Sodhi *et al.*, 2004b). The effect of body size on extinction risk was greater for range-restricted species (Table 5.4). Since large-bodied species tend to exist at lower densities, range-restricted large-bodied species are likely to have small population sizes and will therefore be more likely to be vulnerable to human disturbance (Brown & Maurer, 1987). Interestingly, body weight had no significant effect on local-scale sensitivity to disturbance (Table 5.4). Species were more likely to be threatened if they had a narrow altitudinal range, and this effect was greater for range-restricted species (Table 5.4). This is consistent with Lee *et al.* (2005), who suggested that these species may be unable to avoid disturbance due to physiological intolerance of elevational migration. As with local-scale responses to disturbance, specialists were more likely to be threatened; narrow habitat and/or diet breadth and high forest dependency were associated with higher threat status. However, forest-dependency was much less important for range-restricted species (Figure 5.4b) and there was no significant association with extinction risk for this group of species (Table 5.4). This could indicate that these range-restricted species have already been through an extinction filter (Balmford, 1996); highly forest-dependent, restricted-range species that occur in areas of high forest loss have already gone extinct, so that the remaining restricted-range species are either not dependent on forest or inhabit less impacted regions. Insectivores and herbivores were more likely to be threatened than carnivores, frugivores or omnivores (Table 5.4). It could also indicated that most range-restricted species are forest dependent and so there is less variation in this intrinsic predictor for these species. Of the 499 range-restricted species, 263 (52.7%) are highly dependent on forest (compared to 29.8% of the complete species list used in this study) and only 30 (6.0%) are not known to use forest (compared to 15.3% of all species). Other authors have found that insectivores are more likely to be extinction-prone (e.g. Thiollay, 1995; Castelletta *et al.*, 2000; Zakaria *et al.*, 2005). That omnivores are relatively less threatened is another example of generalists being more resilient than specialists (e.g. Sodhi et al., 2005b; Pocock, 2011). Unlike local-scale responses to disturbance, migratory behaviour did not show a significant association with global extinction risk (Table 5.4). This is contradictory to Sanderson *et al.* (2006), who found that Afro-Palearctic migrants have suffered greater population declines than their non-migratory counterparts. However, this finding was largely driven by the declines in species that winter in open, arid areas in Africa and so species of the tropical forests of South and South-east

Asia will be affected by different processes. In contrast, range-restricted species were more likely to be threatened if they were full or partial migrants or nomads than if they were sedentary or elevational migrants (Table 5.4).

Although extrinsic factors were less important than intrinsic factors in explaining global extinction risk, they were able to explain about 13% of the variance in threat status (Table 5.3). Species with a high proportion of their range with more than 10 people per square kilometre were more likely to be threatened. Countries in South-east Asia with higher human population densities have lost a greater proportion of their forest (Sodhi *et al.*, 2004a) and forest conversion for agricultural expansion is the leading driver of biodiversity loss in South-east Asia (Sodhi *et al.*, 2004a; Wilcove *et al.*, 2013). Species were more likely to be threatened if a greater proportion of their range was agricultural, and this effect was greater for range-restricted and highly exposed species (Table 5.4). Although there are a number of threatened bird species that are dependent on low impact agriculture (Wright *et al.*, 2012), agriculture-driven habitat loss was the fourth most important driver of past avian extinctions globally (after invasive species, hunting and logging) and is the most important threat for extant birds; consequently, the expansion of agriculture is expected to become the most important driver of future avian extinctions (Szabo *et al.*, 2012). It has been suggested that limiting the extent of agricultural land use by combining intensive farming with land sparing, which would minimise the proportion of species' ranges that is used for agriculture, would benefit more species than the land-sharing approach of extensive wildlife-friendly farming (Green *et al.*, 2005; Phalan *et al.*, 2011). Conversely, species were less likely to be threatened if a greater proportion of their range was urban. This could again indicate a past extinction filter; for example, Balmford (1996) found the lowest proportions of threatened species across Mediterranean regions and Pacific Islands where humans have been settled the longest, suggesting that the more sensitive species have already been purged from assemblages.

It might be expected that extrinsic factors are less important in explaining the extinction risk of highly exposed species compared to all species, but the proportion of variance explained was only marginally lower (12.8%) than for all species (13.4%; Table 5.3). One reason for this result, and the lower explanatory power for extrinsic factors compared to intrinsic factors for all the global extinction risk models, might be the location of the study, since IndoMalaya has a limited range of human impact factors; the entire region is highly impacted compared to other realms. Davies *et al.* (2006) found that human population density was the main driver of the global distribution of the number of threatened species. However, when Indo-Malaya was considered separately, human population density did not remain in the final model. They suggest that this is due to Indo-Malaya having both the highest number of threatened species and the highest human population density, which shows little variation across the realm (Davies *et al.*, 2006).

Species with traits associated with sensitivity to disturbance may not necessarily be threatened if their range does not coincide with highly disturbed areas. There is a greater proportion of currently threatened species amongst the avifauna in Borneo, Sumatra and southern Thailand (Figure 5.5b), which is also where there has been high deforestation (Hansen *et al.*, 2013; Figure 5.6). The forested areas in southern China and on Sulawesi have been less disturbed compared to other parts of this region (Hansen *et al.*, 2013; Figure 5.6) and in these areas there is a high proportion of species that are of least concern on the IUCN Red List, but also have high predicted sensitivity using the local-scale disturbance model. In other words, future habitat disturbance in these areas could result in large biodiversity losses because a high proportion of the species here are intrinsically predisposed to sensitivity. Cardillo *et al.* (2004) suggested that we should use intrinsic factors and projections of future human disturbance to predict species that are not currently threatened but may become so in the future in order to identify future conservation needs.

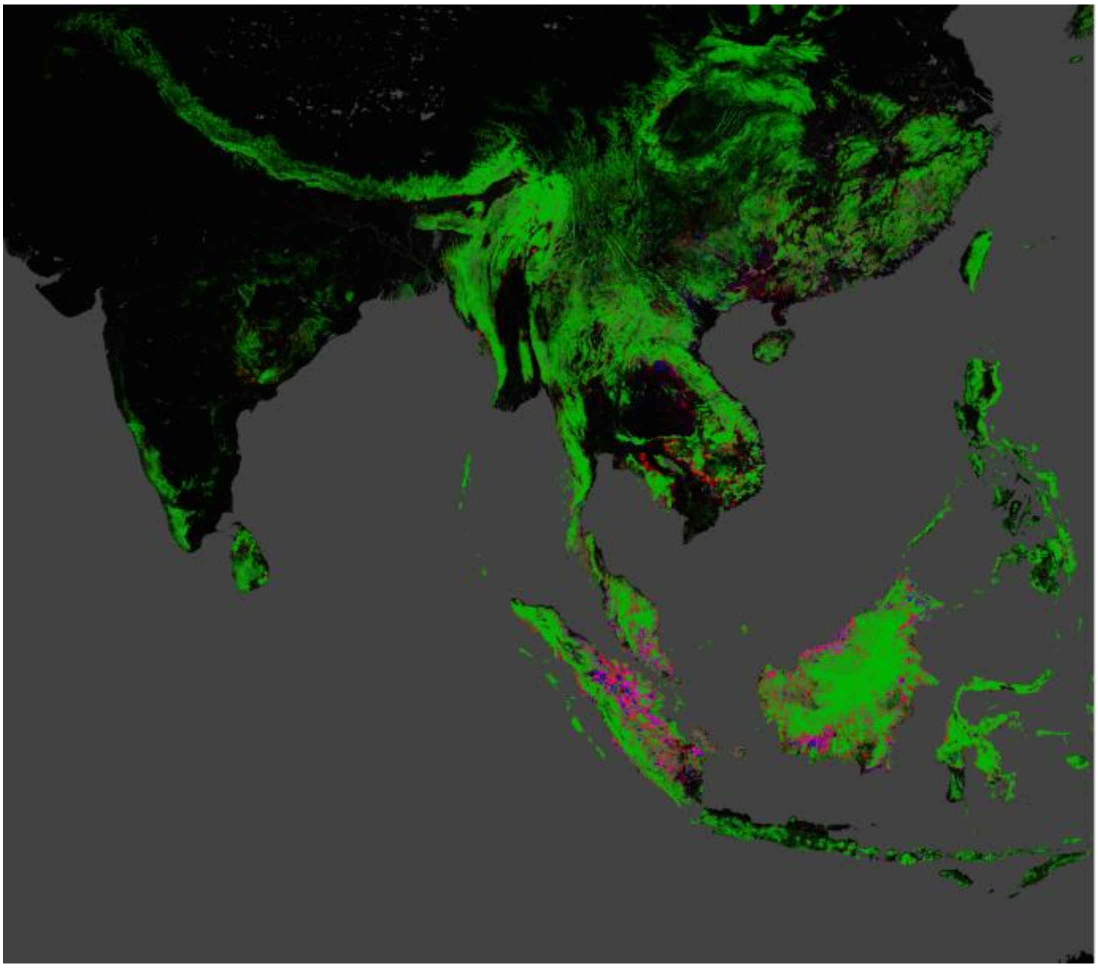

Figure 5.6: The distribution of forest extent, losses and gains across South and South-east Asia: Red = Forest Loss 2000–2012, Blue = Forest Gain 2000–2012, Pink = Both Loss and Gain, Green = Forest Extent. Data from Hansen *et al.* (2013).

5.6 Conclusions

These analyses of South and South-east Asian birds indicate that species' sensitivity to local habitat disturbance varies depending on the type of disturbance, with urban habitats being relatively more disturbing than burning, logging or secondary forest. At large scales, bird species are more likely to be extinction prone if a high proportion of their range has high population density or is under agricultural land use. The importance of intrinsic factors in determining sensitivity to habitat disturbance is more evident at large than local scales. Species are more sensitive at both local and large scales if they are highly forest dependent and/or have a narrow habitat breadth, but the importance of other traits is scale-dependent; body weight, altitudinal range and diet type is more important at large scales and migratory behaviour, development at hatching and the use of manmade sites is more important at local scales. Some species have intrinsic traits that render them sensitive to local-scale disturbance, but inhabit areas comprising less damaged habits and so are not currently threatened. These species could therefore be of conservation concern in the future as agricultural expansion is set to further affect habitats in this region.

Chapter Six: The functional traits of endemic versus widespread species at a global scale

6.1 Abstract

Aim: Species' traits may vary with range size and species with the smallest ranges are less likely to be covered by the protected area network. In this chapter we aim to compare the occupancy of trait space by endemic and widespread species and to identify whether gap species vary in their trait space occupancy compared with species that coincide with protected areas.

Location: Global

Methods: Principal Coordinates Analysis (PCoA) was used to ordinate 9,052 bird species in multidimensional space using data on functional traits related to resource use. Species were separated for comparison into four quartiles from the endemic (smallest 25% of range sizes) up to the most widespread species (largest 25% of range sizes). Shape-files of each species' geographic range were overlaid with the "strictly protected" areas in the protected area network (IUCN categories I-IV) and with BirdLife International's Important Bird and Biodiversity Areas (IBAs) to assess their coverage.

Results: There were significant differences in the mean position of species in of trait space according to geographic range size and protection status; endemic species and gap species were more likely than widespread and protected species respectively to occur in the region of traits space associated with higher habitat strata, higher trophic levels and smaller body mass.

Main conclusions: Since bird species' traits vary with respect to geographic range size and species with smaller range sizes are less well covered by the global protected area network, conservation efforts should be focussed on endemic species and on optimising coverage of functional traits to protect ecosystem processes. One way of extending the protected area network could be to give legal protection to all of BirdLife International's IBAs, which could improve the protection of functional traits since 98.6% of all species would be covered and there would be no significant difference in the position of species in functional trait space with regard to diet and body mass. However, species that occupy higher habitat strata and forage in vegetation may still not be adequately protected in some areas.

Key words: Gap analysis, geographic range size, Important Bird and Biodiversity Areas, principal coordinates analysis, protected area network

6.2 Introduction

The study of the geographic ranges of organisms is a central theme in biogeography (Brown *et al.*, 1996) and a species' geographic range size is one of its most important traits (Gaston, 2003). As with organisms as whole, whose range sizes cover 12 orders of magnitude (Brown *et al.*, 1996), the global distribution of bird species range size is highly skewed; many species have relatively small range sizes and the smallest range sizes are found particularly on islands and in mountainous areas (Orme *et al.*, 2006). This suggests that range size might be a function of the available land area within the species' climatic tolerances. Indeed, the size of a species' geographic range is thought to be largely determined by the distribution of suitable abiotic and biotic conditions (Gaston, 2003). However, species may not have the dispersal ability to colonise all the areas of suitable conditions and other aspects of a species' ecology may also affect its geographic range size. In some taxa, it has been found that closely related species have similar geographic range sizes (e.g. Jablonski, 1987), suggesting that heritable traits related to species' ecology may affect the size of its distribution (Brown *et al.*, 1996) (although others argue that there is in fact little phylogenetic conservatism in many groups (Gaston, 2003; Webb & Gaston, 2003; 2005)).

As well as the relationship between dispersal ability and range size (e.g. Böhning-Gaese *et al.*, 2006), some other aspects of species' ecology have been found to be associated with range size. A number of studies have found a positive association between range size and body size (e.g. Brown & Maurer, 1987; Ayres & Clutton-Brock, 1992), though this relationship is likely to be more complex than a simple linear association; the largest species have the largest range sizes, but small species have a wide variety of range sizes (Gaston & Blackburn, 1996). Consequently, negative (e.g. Glazier, 1980) and non-significant (e.g. Juliano, 1983; Virkkala, 1993) relationships have also been found. The inconsistency of these relationships could also be a result of interactions between traits affecting the direct association between body size and range size (Laube *et al.*, 2013); larger animals interact with the environment at a larger spatial scale and therefore exist at lower densities over a more widespread area (Brown, 1984), but large body size could also be associated with traits that are linked to smaller range sizes such as lower fecundity or reduced dispersal ability (Laube *et al.*, 2013).

The possible associations between geographic range size and biological traits may have some important consequences for conservation. Geographic range size emerged as the strongest predictor of extinction risk in a global analysis of bird species, even after excluding species that were red-listed because of their declining range size (Lee & Jetz, 2011). Species are currently being lost at rates far higher than natural extinction rates (Barnosky *et al.*, 2011) and there is global recognition that we need to reverse this trend. Protected areas (designated geographic areas with legal protection restricting human activities) cover more than 12% of the world's land surface (Jenkins & Joppa, 2009) and are one of the primary methods for conserving species. However, 14.0% of threatened bird species were found to be 'gap species' whose range does not coincide with any protected area (Rodrigues *et al.*, 2004b). Despite the fact that endemism richness is the most important predictor of the coverage of protected areas (Loucks *et al.*, 2008), species with the smallest ranges (endemics) are more likely to be gap species (Rodrigues *et al.*, 2004b). More recently, a global study of birds found that a greater proportion of a species' range is protected if that species has a large geographic range (Cantú-Salazar *et al.*, 2013). Restricted-range species show greater variability in the proportion of range protected since they have a greater tendency for either none or all of the range to fall within a protected area (Cantú-Salazar *et al.*, 2013). Given the gaps in protection of narrow-ranging species, an important conservation issue therefore concerns whether or not narrow-ranging species are distinct in terms of the functional ecological roles they perform in ecosystems.

The Convention on Biological Diversity's Strategic Plan for Biodiversity includes a target to have at least 17% of terrestrial surface area protected by 2020 (CBD, 2010). The expansion of the protected area network should target areas that have been identified as being of high conservation value in order to be most effective (Rodrigues *et al.*, 2004a). One of the largest schemes to identify such areas is BirdLife International's 12,000 "Important Bird and Biodiversity Areas" (IBAs), many of which are home to threatened and restricted-range species (Birdlife International, 2013). Nearly half of these sites do not coincide with protected areas and therefore have no legal protection. Butchart *et al.* (2012) showed that birds of conservation interest that occur in IBAs with less than 50% of their area protected have increased their extinction risk at twice the rate of those species occurring in IBAs where the majority of the area is protected. If IBAs are also home to species with traits that are under-represented by the current protected area network, then protecting these regions could conserve important ecological roles.

In this chapter, we use a global database of avian traits (9,052 species) to identify differences between species associated with their range size. We use multivariate techniques to compare the occupancy of trait space of endemic versus widespread species. We perform a gap analysis to identify species not currently protected by the global protected area network in order to assess if some traits may be less well protected. We then ask if we would improve the protection of traits if we protected areas identified as IBAs by BirdLife International.

6.3 Methods

6.3.1 Bird species distributions

Analyses of species' distributions and protected areas were carried out using ArcMap 9.3 (ESRI, 2010). Shape-files of species' ranges were provided by BirdLife International (Birdlife International & Natureserve, 2011). These polygon maps are based on known locations (e.g. geo-referenced point locality records, collecting locality of museum specimens) and expert opinion (see Buchanan *et al.*, 2011 for details). For each species, the areas in which it is considered extant or probably extant throughout the year and those in which it is present only in the breeding season were included separately and areas where it was considered possibly extant or possibly extinct or where its presence was uncertain were excluded. Sea birds, defined as those species that predominately feed at sea and are described as pelagic or feeding offshore (Del Hoyo *et al.*, 1992; 1996), were excluded from the analysis. The exclusion criteria were consistent with those used in other macroecological analyses of bird distributions (e.g. Orme *et al.*, 2006).

The range maps of birds were sampled on a grid using the Behrmann cylindrical equal-area projection. The cell resolution was 96.486 km x 96.486 km, equivalent to 1° longitude and approximately 1° latitude at the equator, which created 15,655 cells with >50% land area; each cell comprised all those species whose ranges overlapped with the grid cell. The geographic range size was calculated in ArcMap 9.3 in square kilometres. Species were separated into four quartiles according to range size from the endemic (smallest 25% of range sizes) up to the most widespread species (largest 25% of range sizes). There were 2,263 species in each of these groups.

6.3.2 Protected Area Network and Important Bird Areas

We used the most recent version of the World Database of Protected Areas (WDPA) (IUCN & UNEP-WCMC, 2013). We only included protected areas with a status of "designated", i.e. we excluded proposed protected areas. Not all protected areas offer equal protection to species; the IUCN categorises protected areas in one of six Protected Area Management

Categories (IUCN, 1994). Categories I-IV are considered to be “strictly protected” (e.g. Jenkins & Joppa, 2009; Rodrigues *et al.*, 2004b). Protected areas in categories V and VI allow human activity, including sustainable management of natural resources. Therefore, we included only the “strictly protected” areas in our gap analysis. Although other analyses of protected area coverage have included protected areas in all the IUCN management categories (e.g. Rodrigues *et al.*, 2004b; Cantú-Salazar *et al.*, 2013), some authors have compared overall coverage with that of the stricter IUCN categories; Rodrigues *et al.* (2004b) found that 37.3% of threatened species did not coincide with a protected area of at least 1000km^2 in IUCN categories I-IV. There were 73,611 designated protected areas in IUCN categories I-IV for which a polygon shape-file was available. Additionally, there were 13,361 point locations with documented extent of the protected area. Therefore we included these sites by creating a buffer around the point that was equal to the documented extent, assuming that the point represented the centre of the protected area. This is consistent with methods of other studies where protected areas are only represented by point data (e.g. Rodrigues *et al.*, 2004b); eliminating point locations from the dataset would create bias since some locations have a greater number of protected areas without polygon shape-files (Jenkins & Joppa, 2009). Overall, this meant that 86,972 protected areas were included in our analyses. We considered a species to be a gap species if its geographic range did not overlap with a protected area in categories I-IV. Shape-files of the Important Bird and Biodiversity Areas (11,370 polygons) were obtained from BirdLife International.

6.3.3 Functional traits

For our analysis of functional traits, we selected those related to resource use (Table 6.1). Feeding location, strata used and diet were considered as binary traits since the categories are not exclusive e.g. a bird could feed both on the ground and in vegetation. Trait values for each species were collated using a variety of sources (listed in Appendix S1: Sources used for bird trait data). Where data were not available for individual species (<10% of species-trait combinations), genus, or failing that family, values were used (Table 6.1).

Principal Coordinates Analysis (PCoA), also known as multidimensional scaling (Gower, 1966), was used to describe the distribution of species within the overall functional trait space. PCoA is similar to Principal Components Analysis (PCA), but it can be used for traits which are not measured on a continuous scale. The PCoA is used to ordinate species along axes representing variation in associated sets of traits so that the distances between species are approximately equal to the dissimilarities in their trait values. The trait vectors and factors were fitted to the PCoA to identify which functional traits are most important in differentiating between species in terms of their functions.

6.3.4 Statistical analyses

The PCoA dimension scores were compared between range size quartiles using ANOVA and Tukey's Honestly Significant Differences post-hoc test. The PCoA dimension scores were compared between protected and gap species using t-tests. Computation of PCoA and all statistical analysis was carried out using R version 2.12.0 (R Development Core Team, 2010).

Table 6.1: Functional traits used for calculating functional diversity.

Trait	**Type**	**% Species-trait combinations using averages**	
		Genus	**Family**
Weight ($\log_e$ grams)	Continuous (1.61-11.62)	8.2	0.8
Circadian activity	Categorical (Diurnal, nocturnal, crepuscular, all times)	5.9	1.9
Feeding group size	Ordinal (1, 2-6, 6-10, 10-20, 20-50, >50 individuals)	12.0	3.1
Feeding location(s)	Binary (Ground, water, vegetation, aerial, on other animals)	7.1	0.6
Strata used	Binary (Ground/water, grass/low vegetation, shrub layer/understorey, mid-storey, canopy or above)	8.9, 9.5*	0.8, 1.1
Diet	Binary (Vertebrates, invertebrates, fruit & berries, seeds & nuts, nectar & sap, foliage & other plant parts, e.g. roots)	5.7	0.4

*Genus averages were used for 8.9% of species for the highest stratum used and 9.5% for the lowest stratum; species are assumed to use all the strata in between their highest and lowest heights.

6.4 Results

PCoA dimensions one to four explained 31.2%, 16.0%, 14.2% and 8.3% of variation, respectively. The later dimensions were not considered because they each explained less than 7% of the variance and did not show clear and interpretable trait associations. Positive scores of dimension one were associated with activity in low habitat strata (ground/water to grass/low vegetation) and foraging on the ground, whereas negative scores of dimension one were associated with activity in high habitat strata (middle layers to canopy or above) and foraging in vegetation (Figure 6.1a). Hence the greatest variation among species traits was found to be for habitat strata used and where species forage. Positive scores of dimension two were associated with foraging on or in water and negative scores were associated with activity in grass/low vegetation, shrubs/understorey and the middle layers; therefore this dimension separated species according to an aquatic-terrestrial divide (Figure 6.1a). Positive scores of dimension three were associated with herbivorous feeding (mainly seeds or nuts, fruit or berries and vegetation or other plant parts). Negative scores were most strongly associated with foraging in the air and feeding on vertebrates or invertebrates; therefore this dimension separated species according to a carnivory-herbivory gradient (Figure 6.1b). Positive scores of dimension four were most strongly associated with body size, followed by feeding on vertebrates and foraging on or in the water. Negative scores were associated with feeding on invertebrates (Figure 6.1b); therefore this dimension separates species according to body size and prey size.

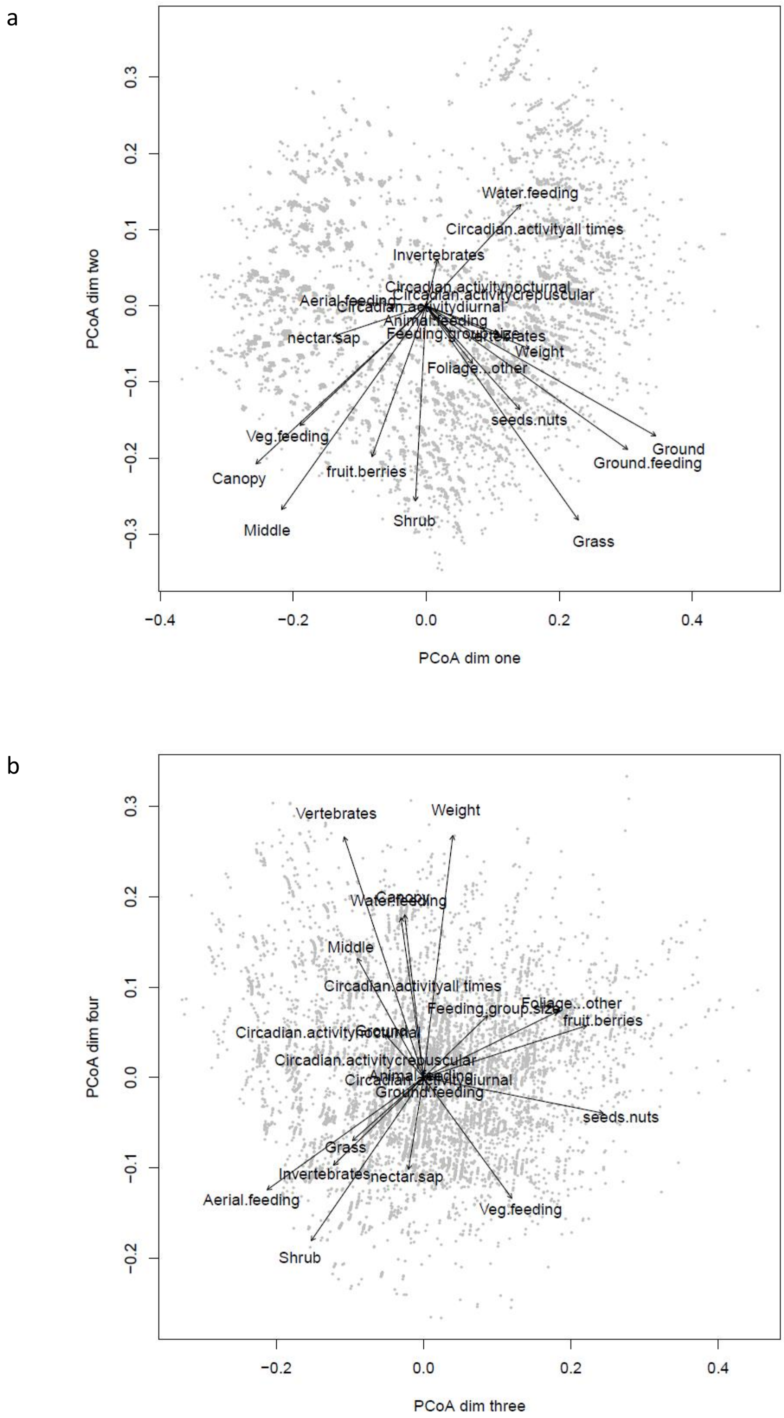

Figure 6.1: Dimensions (a) one and two and (b) three and four of the Principal Coordinates Analysis (PCoA) of traits related to resource use (9,052 species). Each point is one species in functional trait space.

The differences in geographic range sizes for species separated into quartiles from endemic to widespread species can be seen in Figure 6.2. When the distribution of species in trait space is considered separately for these four quartiles, it can be seen that there are differences in the position of species in trait space (Figure 6.3). There were subtle but significant differences between the PCoA scores for species in the four quartiles; in all four dimensions considered, the endemic species were significantly different from the most widespread species (Figure 6.4). When PCoA dimensions one and two are plotted, there is a greater density of widespread species in the bottom right-hand quadrant, which is the part of the trait space associated with low habitat strata and terrestrial foraging, whereas endemic species are more evenly distributed (Figure 6.3a,d). By comparing the mean values of these two groups, these results suggest that endemic species are more likely to use higher habitat strata (low dimension one scores) and to forage in or on water (higher dimension two scores; Figure 6.4).

In order to check these results, the proportions of endemic and widespread species with certain traits was tested. Roughly half (47.2%) of endemic species use the ground/water (i.e. the lowest habitat stratum), whereas nearly three-quarters (73.3%) of the most widespread species use this stratum. Additionally only 40.7% of endemic species forage on the ground, whereas 58.5% of widespread species forage here. Approximately half of both endemic (48.2%) and widespread (48.6%) species use the canopy or higher habitat strata. Therefore, rather than endemic species being more common at higher habitat strata, it appears that they less likely to be found at lower strata and are therefore restricted to higher habitat levels. Indeed, on average they occur in fewer habitat strata (out of a possible 5: ground/water, grass/low vegetation, shrub layer/understorey, middle layers and canopy or above) than widespread species (95% CI: 2.71-2.81 versus 3.21-3.32). Nearly three-quarters (74.2%) of endemic species forage in vegetation, compared to 57.5% of widespread species. Therefore, both the PCoA analysis and the prevalence of individual traits support the result that endemic species are more likely to be restricted to higher habitat strata and to forage in vegetation rather than on the ground. However, the data on water foraging do not support the interpretation of the PCoA result; 5.2% of endemic species forage in/on water, compared to 19.3% of widespread species.

When PCoA dimensions three and four are plotted, there is a greater density of endemic species in the bottom right-hand quadrant, which is associated with herbivory and small body weight, whereas there are more widespread species in the region of trait space associated with carnivory (Figure 6.3e,h). Analyses of mean positions suggest that on average, endemic species are more likely to be herbivorous (higher dimension three scores) and to have small body mass (lower dimension four scores; Figure 6.4). Examination of the prevalence of certain diet items partially supports the interpretation of dimension three; 31.9% of widespread species feed on vertebrates, compared to just 10.3% of endemic species. There is only a small difference in the proportion of species that feed on fruit/berries; 38.4% of endemic species feed on fruit or berries, compared to 34.1% of widespread species. Out of the possible six diet items recorded (vertebrates, invertebrates, fruit & berries, seeds & nuts, nectar & sap and foliage & other plant parts), widespread species had a greater diet breadth than endemic species (95% CI: 2.14-2.23 versus 1.79-1.86). Taken together, these results suggest that endemic species are more likely to be restricted to lower trophic levels. Endemic species have on average smaller body weight than widespread species (95% CI: 3.62-3.75 versus 4.19-4.33 $\log_e$ grams).Mapping the proportion of endemic species and the mean score for each of the PCoA dimensions in each grid cell reveals that the associations between endemism and position in trait space are different between biogeographical regions. Regions of high levels of endemism and species being associated with higher habitat strata on average can be seen in tropical forested regions, e.g. tropical Andean region, riverine areas of Brazilian Amazon, African Rift, New Guinea, Sundaland and the Himalayas (blue regions on Figure 6.5a). However, there are also regions of high endemism and species associated with lower habitat strata. These are mainly concentrated in arid regions, e.g. the Atacama and Namib deserts (black regions on Figure 6.5a). Regions of high levels of endemism and species that occur in the region of trait space associated with foraging in aquatic habitats are mainly found in the Neotropics, Madagascar and Sundaland (black regions on Figure 6.5b), whereas other regions of high endemism are associated with species that forage in terrestrial habitats, e.g. Central America, African Rift, Himalayas, Australia (blue regions in Figure 6.5b). Regions of high levels of endemism and species associated with lower trophic levels are found in the Neotropics, New Guinea and the Eastern Himalayas (black regions in Figure 6.5c), whereas regions of high endemism in the Afrotropics, Madagascar and Western India tend to be associated with higher trophic levels (shown in blue in Figure 6.5c). Regions of high endemism tend to be associated with smaller bodied species (blue regions in Figure 6.5d), with the exception of certain drier areas of the Afrotropics, Eastern India and Central Asia, and islands (Madagascar, Sulawesi, New Zealand and the Caribbean) which are associated with high body weight (shown in black on Figure 6.5d).

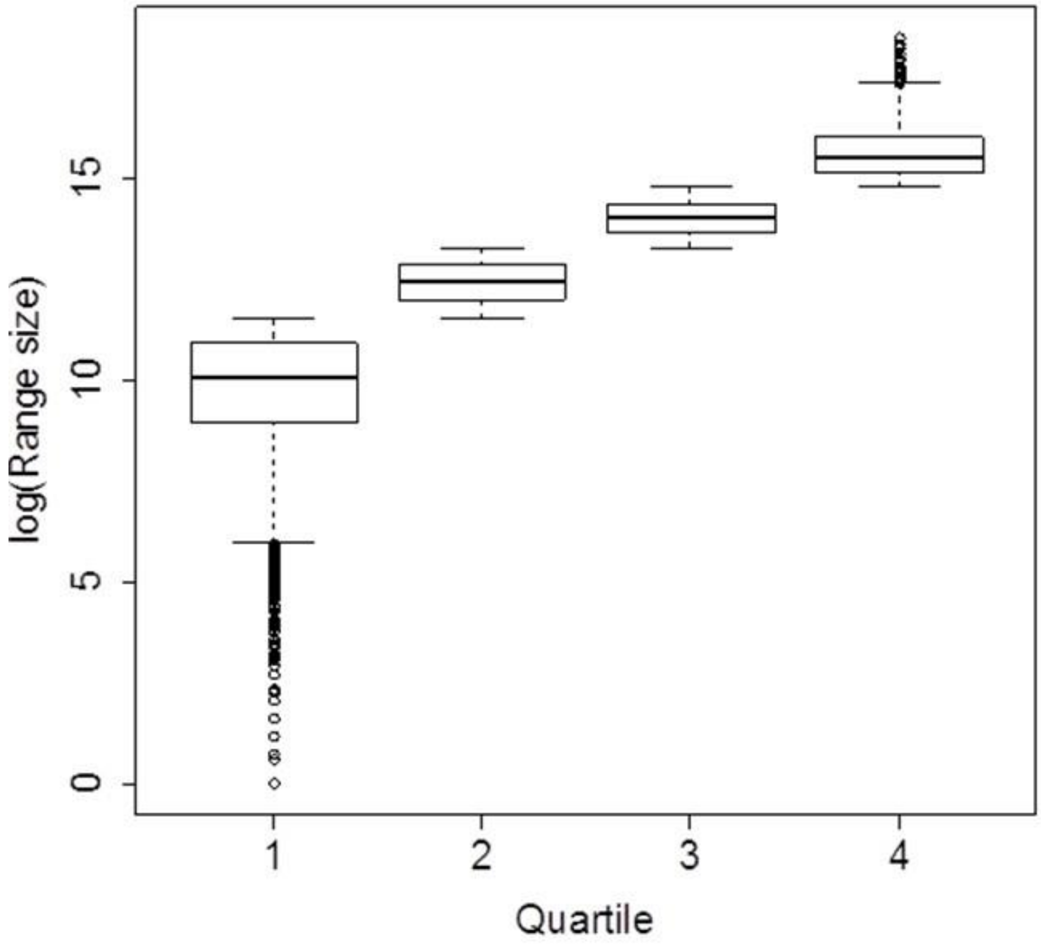

Figure 6.2: The range size ($\log_e$-transformed km^2) of 9,052 birds across the World, divided into quartiles.

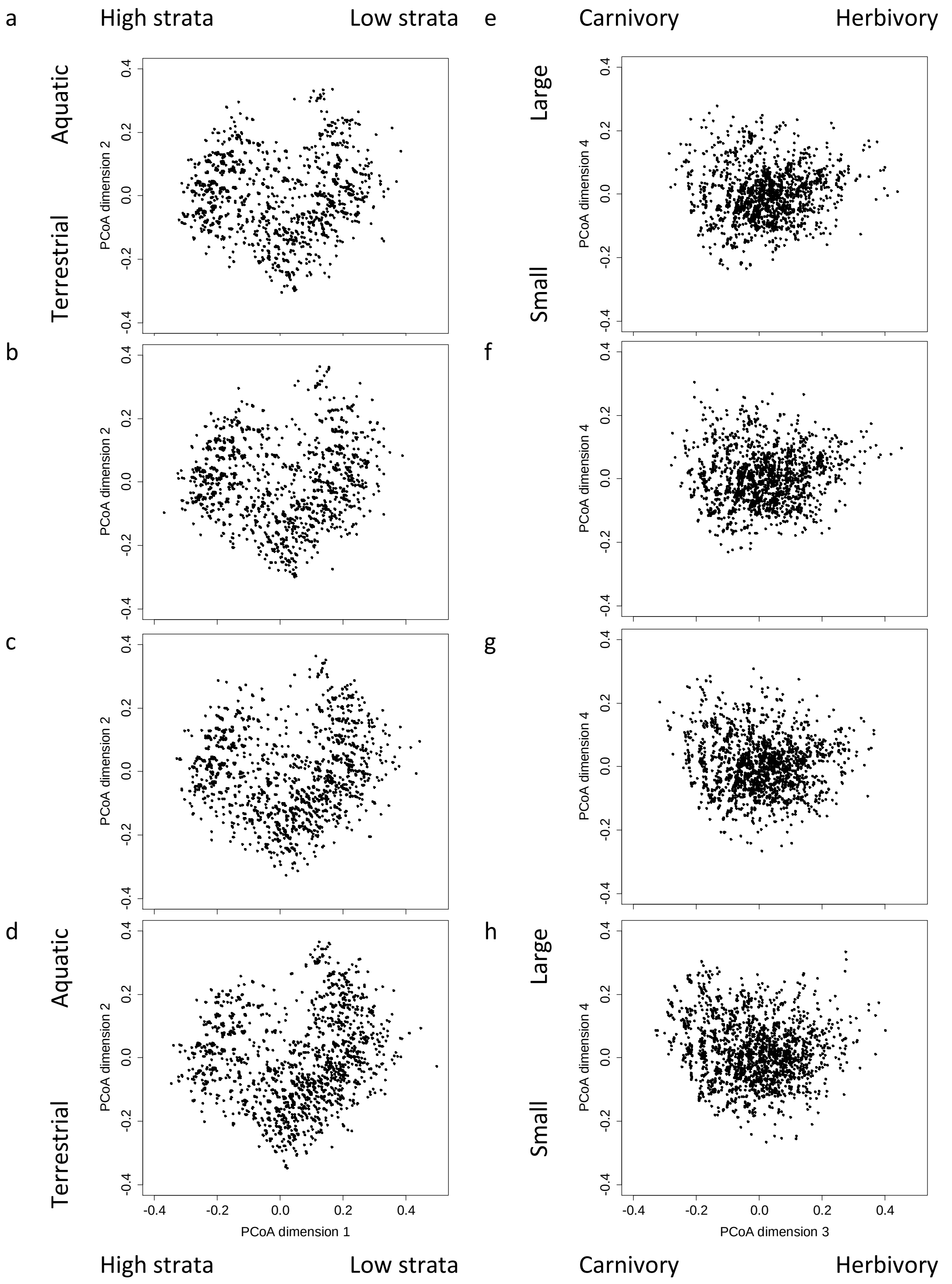

Figure 6.3: The distribution of species in ecomorphological trait space. (a-d) Princpal coordinates analysis (PCoA) dimensions one and two and (e-h) PCoA dimensions 3 and 4. Species are separated according to range size: (a,e) 1st quartile (endemics); (b,f) 2nd quartile; (c,g) 3rd quartile; and (d,h) 4th quartile (widespread). The ordination was performed on traits related to resource use (9,052 species)

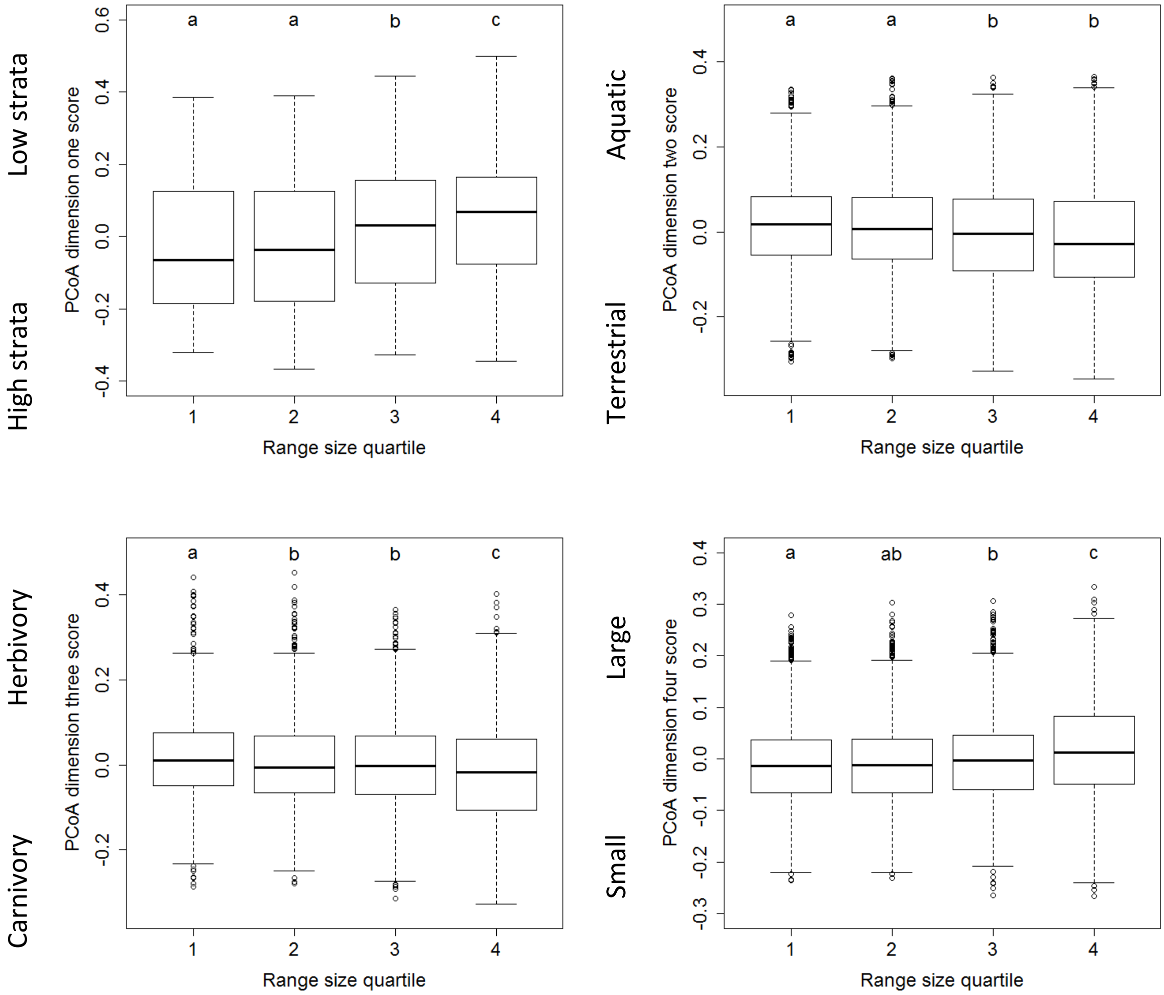

Figure 6.4: PCoA scores for bird species of different range sizes, from the first quartile (endemic species) to the fourth quartile (most widespread species). There are significant differences in the scores of (a) PCoA dimension one $F_{3,9048}$ = 105.6, p<0.0001, (b) PCoA dimension two $F_{3,9048}$ =25.4, p < 0.0001, (c) PCoA dimension three $F_{3,9048}$ = 34.5, p < 0.0001 and (d) PCoA dimension four $F_{3,9048}$ = 57.6, p < 0.0001. Letters indicate significantly different groups (p<0.05) using Tukey's Honestly Significant Differences Test.

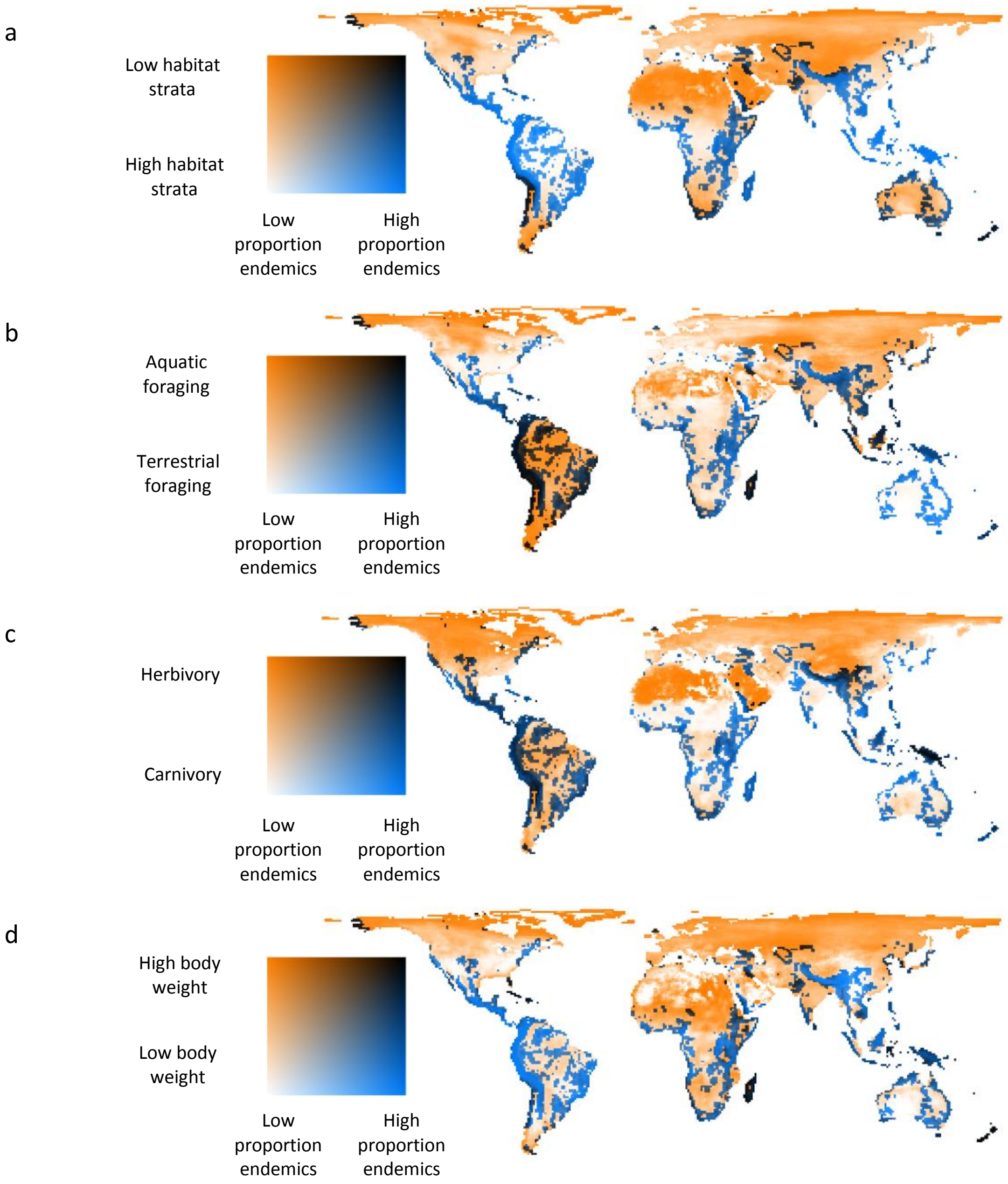

Figure 6.5: The distribution of the proportion of endemics in total species richness and mean PCoA dimension scores. Blue and black regions have a high proportion of endemics. Orange and white regions have a low proportion of endemics. (a) In blue and white regions species are more likely to use high habitat strata. In black and orange regions species are more likely to use low habitat strata. (b) In blue and white regions species are more likely to forage in terrestrial habitats. In black and orange regions species are more likely to foraging in aquatic environments. (c) In blue and white regions species are more likely to be carnivorous. In black and orange regions species are more likely to be herbivorous. (d) In blue and white regions species are on average smaller. In black and orange regions species are on average bigger.

There were 383 species whose range does not fall into one of the protected areas in IUCN categories I-IV (4.2% of all species analysed; see Supplementary Table 11). These had smaller ranges than protected species (median values 7,802km² versus 666,066km²). The largest geographic range size of a gap species was that of the White-browed Chinese Warbler (*Rhopophilus pekinensis*), which covered 1,709,861km². Indeed, the gap species with the largest ranges were found in China, e.g. Claudia's Warbler (*Phylloscopus claudiae*), Rufous-necked Snowfinch (*Montifringilla ruficollis*) and Yellow-bellied Tit (*Parus venustulus*). There were a high number of gap species in China, despite low endemic richness (Figure 6.6a,b). However, other areas with gap species were also sites of high endemism, e.g. New Guinea and the Andes. If IBAs were given the same level of legal protection, then the distribution of gap species would be much more restricted, but there would still be gap species in Mexico and Papua New Guinea in particular (Figure 6.6c). There were significant differences between the PCoA scores for protected and gap species for dimensions 1, 3 and 4 (Figure 6.7), which suggested that gap species were on average more likely to occur in the region of trait space associated with high habitat strata, herbivory and small –body weight. If IBAs were given the same level of protection as protected areas in IUCN categories I-IV, then a further 252 species would be protected, meaning that 98.6% of all species would be covered. There would be no significant difference between dimension scores of gap and protected species for dimensions 2-4, although there would still be a significant difference for dimension one ($t=3.93$, $df=133.74$, $p < 0.001$; Figure 6.7e-h), indicating that the remaining gap species could be more likely to use high habitat strata and forage in vegetation rather than on the ground.

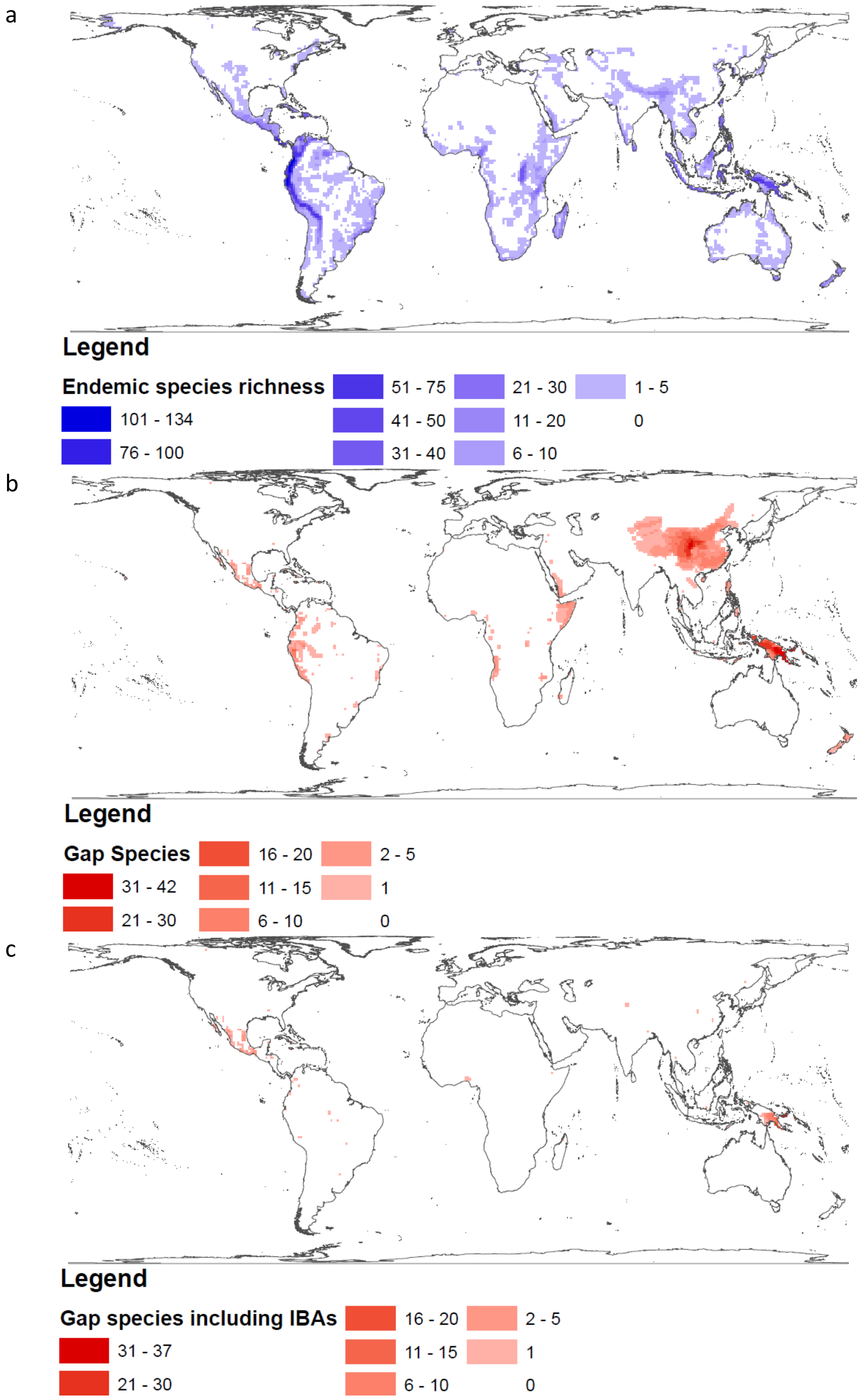

Figure 6.6: The distribution of (a) endemic species richness (species with the smallest 25% of geographic range sizes), (b) gap species (species whose geographic range does not overlap with a protected area in IUCN categories I-IV) and (c) species that would still be gap species if IBAs were all given legal protection in IUCN categories I-IV.

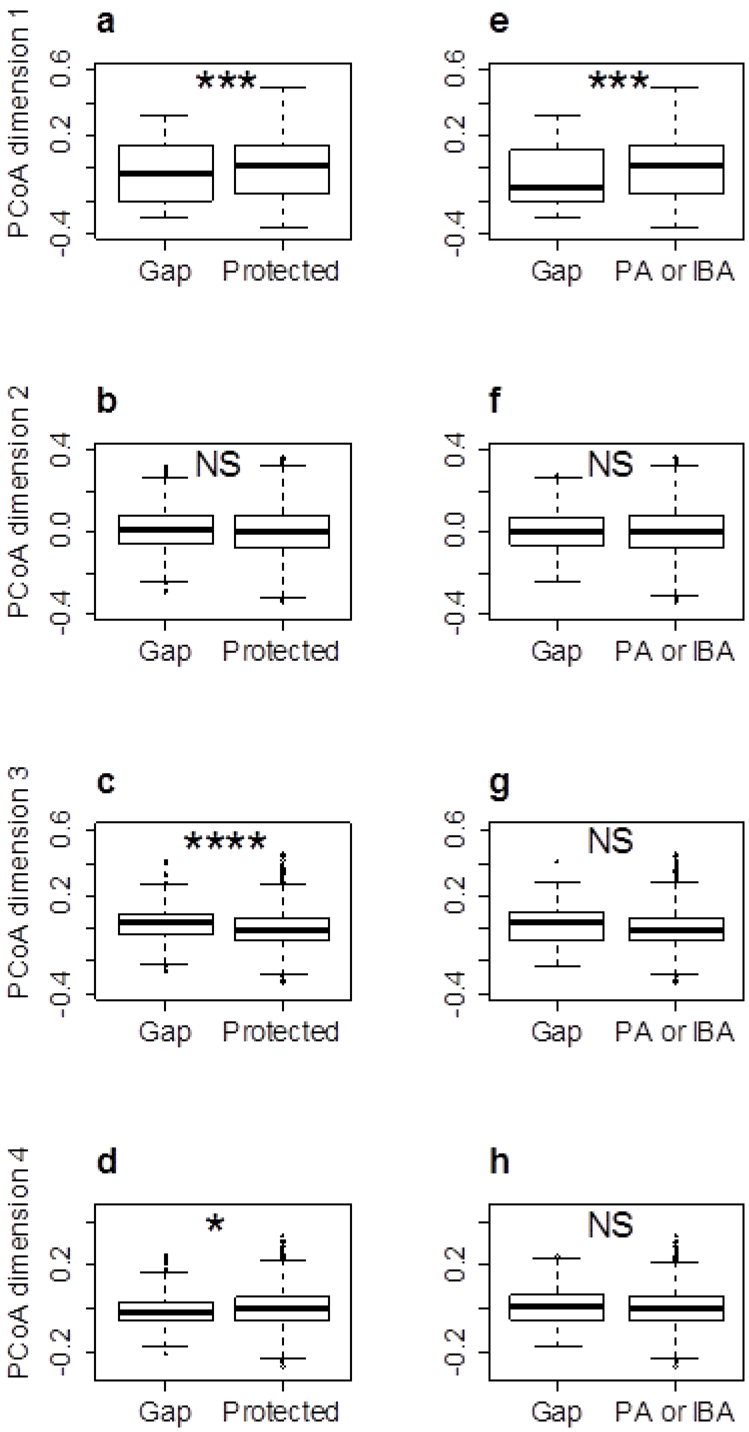

Figure 6.7: The PCoA scores for (a) species that are present in protected areas categories IUCN I-IV and gap species (b) species that would be present in protected areas categories IUCN I-IV if all IBAs were given that level of protection and those that would remain as gap species. Significance values: **** p<0.0001, *** p<0.001, ** p<0.01, * p<0.05, NS Non-significant.

6.5 Discussion

This study found that there were subtle but significant differences between the occupation of trait space by endemic versus widespread species. Since areas of high endemism are also areas of high climate stability (Sandel *et al.*, 2011), and therefore low extinction rates, the differences in traits could be a result of endemic species being adapted to conditions in these refuges, typically regions of topographic heterogeneity such as the Andean Ridge and the Himalayas. As there are imperfect correlations between each of the traits and any of the PCoA dimensions, which in turn explain relatively low amounts of variation, care must be taken in interpreting these results in terms of the associations between range size and any individual trait. On average, endemic species were found to be located within the region of trait space associated with higher habitat strata, water foraging, more herbivorous diet and smaller body size whereas widespread species were on average located within the region of trait space associated with lower habitat strata, terrestrial foraging, more carnivorous diet and larger body size. However, an endemic species is unlikely to reflect all of these traits. Although examination of the prevalence of traits associated with habitat strata and feeding ecology provided additional support that endemic species are more likely to be restricted to higher habitat strata and lower trophic levels and to forage in vegetation, there was a much higher proportion of widespread species (18.2%) that forage in/on water compared to endemic species (5.3%). As identified by Gaston and Blackburn (1996), the associations between range size and traits are rarely linear or simple. Indeed, the relationship between body size and range size in this study reflects the triangular pattern they described (Figure 6.8).

Endemic species were more likely to be restricted to higher habitat strata such as the middle layers or the canopy than widespread species (lower PCoA dimension one scores; Figure 6.4) and species that use these upper layers must inhabit forest habitats. BirdLife International has identified 356 endemic bird areas, where the distributions of two or more restricted-range species coincide, and 83% of the habitat in these sites is forest (http://www.birdlife.org/datazone/eba). Additionally, examination of the maps of the distribution of median range sizes produced by Orme *et al.* (2006) shows that species with smaller ranges tend to be found in forested areas, e.g. Congo Basin and Malay archipelago. An analysis of the endemic avifauna of São Tomé Island showed that endemic species were associated with forest habitats and that the shift from endemic communities to non-endemic communities was mostly associated with decreased canopy cover (De Lima *et al.*, 2013).

Almost all areas with high endemism were also associated with species occupying the region of trait space associated with high habitat strata, with exceptions in arid regions (Figure 6.5a). These exceptions reflect the lack of habitat complexity in these regions; species cannot inhabit the canopy in treeless habitats.

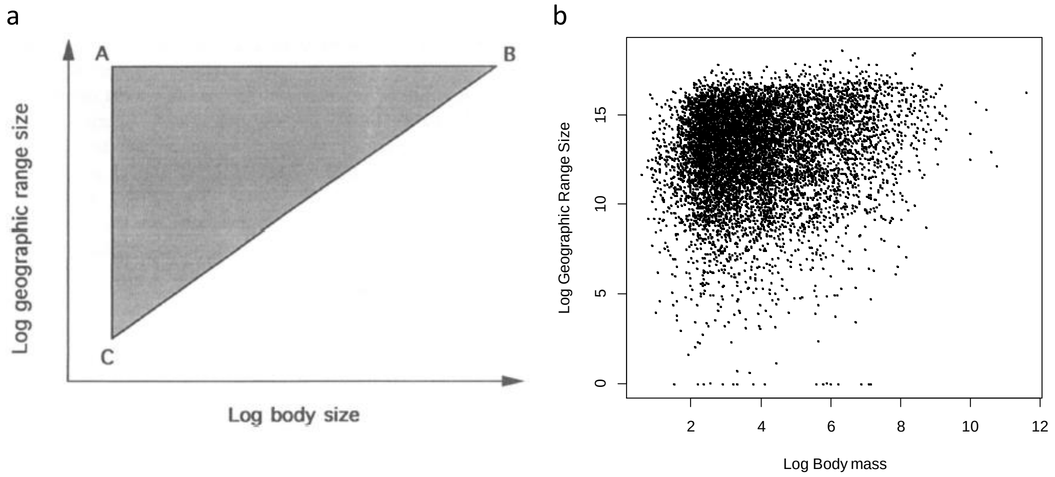

Figure 6.8: (a) Idealised interspecific geographic range size to body size relationship reproduced from Gaston & Blackburn (1996). (b) The relationship between geographic range size (loge km2) and body mass (loge kg) for birds across the globe (9,052 species).

Endemic species had on average higher dimension two scores (Figure 6.4), than widespread species, which implied that they were more likely to be associated with aquatic foraging. However, inspection of this trait in isolation revealed that only 5.2% of endemic species foraged in or on water, compared with 19.3% of widespread species. Therefore interpretation of this dimension was problematic. Although there were significant differences between the range size quartiles, the difference was the smallest compared to the other PCoA dimensions (Figure 6.4). Additionally, although there were regions where high endemism and high values of PCoA dimension two co-occurred (mainly in the Neotropics, Madagascar and Sundaland - black regions on Figure 6.5b), there were also many regions where high endemism and low average values of PCoA dimension two, associated with terrestrial habits, co-occurred (including Central America, African Rift, Himalayas, Australia - blue regions in Figure 6.5b). Traits other than aquatic foraging influence species' positions on this dimension. For example, high values on this dimension may also indicate that species do not forage on the ground (i.e. 59.3% of endemic species versus 41.5% of widespread species), since this trait is negatively correlated with this dimension. The influence of several traits on each dimension should be taken into account when making conclusions based on average dimension scores.

Endemic species were more likely to be restricted to the region of trait space associated with lower trophic levels (higher dimension three scores; Figure 6.4), but this showed biogeographical differences (Figure 6.5c). In contrast to these results, it has previously been suggested that species at higher trophic levels such as insectivores have smaller geographic ranges because the lower availability of food biomass limits their local abundance (Gaston, 1994). However, birds that consume vertebrates tend to be large-bodied, widespread species. Our findings were in contrast to Laube *et al.* (2013), who found that birds with smaller geographic ranges were associated with higher trophic levels. Their study comprised only 165 European passerines and they acknowledged that they may have found different conclusions had they included carnivorous species that feed on vertebrates, such as birds of prey, which generally have large geographic ranges. For example, in our study there were 230 members of the Accipitridae family (hawks and eagles) which had a median geographic range size of 3.9 million km^2; 134 of these were classified as the most widespread species in this study.

On average, widespread species were larger-bodied than endemic species (higher dimension four score; Figure 6.4), which is consistent with a number of studies that have found that widespread species are associated with larger body sizes than restricted-range species (e.g. Brown & Maurer, 1987; Ayres & Clutton-Brock, 1992; Gaston & Blackburn, 1996). There are a number of proposed mechanisms for this relationship. It could reflect a greater chance of extinction for small-ranging, large-bodied species due to them being at lower densities and therefore having a small total population size, i.e. a larger minimum geographic range for a viable population size (Brown & Maurer, 1987; Gaston & Blackburn, 1996). Alternatively, larger species are better able to cross geographical boundaries and/or disperse (Ayres & Clutton-Brock, 1992; Gaston & Blackburn, 1996). It may also be incidental due to both body size and geographic range size increasing with latitude (Gaston & Blackburn, 1996). The tendency for regions of high endemism to be associated with smaller body size was contradicted on islands such as Madagascar, Sulawesi, New Zealand and the Caribbean (Figure 6.5d). The 'island rule' was first proposed by Foster (1964) based on an observation that mammal species that are small on the mainland have larger counterparts on islands (and vice versa). This has also been found to be the case for birds (Clegg & Owens, 2002) and the explanation for larger counterparts of small mainland species being found on islands is thought to involve increased intraspecific competition at high island population densities.

Since the occupation of trait space has been shown to vary with geographic range size and species with small ranges are more likely to be gap species, it is not surprising that there are significant differences between the occupation of trait space by protected and gap species. Gap species were more likely to occur in the region of trait space associated with higher habitat strata (low dimension one values) and this would still be the case even if protected areas were extended to cover all IBAs (Figure 6.7a,e). Gap species were more likely to occur in the region of trait space associated with feeding at lower trophic levels than protected species (higher dimension three scores; Figure 6.7c). The loss of herbivorous species from an ecosystem could have damaging consequences for ecosystem processes, since these species could contribute to seed dispersal (frugivores) or pollination (nectarivores) (Şekercioğlu *et al.*, 2004). If IBAs were given the same legal protection as the protected areas considered in this study, then there would be no significant difference in distribution of protected and gap species along the carnivory-herbivory gradient. Protected species were more likely to occur in the region of trait space associated with large body size than gap species (higher dimension four score; Figure 6.7d). In spite of this, small body size has been associated with a lower risk of extinction than large-bodied animals (e.g. Owens & Bennett, 2000; Sodhi *et al.*, 2004b; Peh *et al.*, 2005; Gaston & Blackburn, 1995), with possible explanations including larger species having smaller population sizes and being present at lower densities (Sodhi *et al.*, 2004b; Gaston & Blackburn, 1995), requiring greater habitat or diet resources (Gaston & Blackburn, 1995) or being more vulnerable to human persecution (Owens & Bennett, 2000).

Although more than 95% of the species in our analysis overlapped with protected areas, this does not mean that these species are necessarily adequately protected, since only a small proportion of the range would need to coincide with a protected area in order for the species to be classified as protected. Rodrigues *et al.* (2004a) suggested that there should be a target for the proportion of a species' range that is protected based on the size of its extent of occurrence (EOO); 100% of the range should be protected for narrow-ranging species (EOO < 1,000km^2), 10% of the range should be protected for wide-ranging species (EOO > 250,000km^2), and the target for intermediate species can be calculated using linear interpolation. Using these criteria less than half (~46%) of bird species are adequately protected and only about 8% of birds with the smallest ranges (lowest quartile) reach their target level of protection (Cantú-Salazar *et al.*, 2013). Furthermore, these values were calculated using all protected areas without discriminating according to IUCN management category (Cantú-Salazar *et al.*, 2013). Indeed, despite the increase in the coverage of protected areas, pressures on biodiversity are increasing and the rate of biodiversity loss is not lessening (Butchart *et al.*, 2010). Therefore, new protected areas should be located in areas of high conservation value in order to improve the effectiveness of the network (Rodrigues *et al.*, 2004a). We found that if BirdLife's IBAs were given the same level of protection as the PAs in this study, there would be no significant differences in the mean position in trait space of protected versus gap species for three out of the four ordination dimensions. Therefore protecting these areas would improve the protection of species' traits. However, there would still be a significant difference in the scores of PCoA dimension one (which explains nearly a third of the variance of the species in trait space), indicating that species restricted to higher habitat strata may be under-represented in some places. Canopy species are an important part of the forest food web and canopy insectivores have been shown to provide a central role in pest control that reduces leaf damage (Van Bael *et al.*, 2003; Recher & Majer, 2006; Murakami & Nakano, 2000).

The crude measures of the range of habitat strata used and diet breadth in this study suggested that endemic species are more likely to be specialised than widespread species. This is consistent with other studies that have found that species with a narrower habitat breadth have smaller geographic range sizes (Hurlbert & White, 2007; Carrascal *et al.*, 2008; Laube *et al.*, 2013); species that can utilise a wider range of habitats that span a greater range of conditions can inhabit larger geographic areas. Although there were significant differences between widespread and endemic species in their mean positions in trait space, these differences were subtle and it is worth noting that there was substantial overlap in the range of dimension scores represented across each of these groups. From a historical perspective, this overlap may reflect that species' range sizes respond readily to climate shifts in a way that is relatively independent for most ecological traits. Conversely, the finding that endemic species are associated with areas of high climate stability (Sandel *et al.*, 2011), suggests that endemics have particular traits that make them more sensitive to the speed of climate change. Evidence for the latter is perhaps only weakly supported by the results of this study. However, it is also possible that some of the more climate-sensitive traits have been omitted from our analysis. This is an interesting topic for further exploration.

6.6 Conclusions

In conclusion, we have demonstrated that there are subtle but significant differences in the region of trait space occupied by bird species with different geographic range sizes, which could have conservation implications since species with smaller range sizes are less well covered by the global protected area network. Since the diversity of traits represented by species in a community could affect ecosystem processes, protected areas are needed in areas of high endemism where narrow-ranging species could be relatively more important for these processes. One way of extending the protected area network could be to give legal protection to all of BirdLife International's IBAs, which would improve the protection of functional traits. However, species that occupy higher habitat strata and forage in vegetation may still not be adequately protected in some areas.

Chapter Seven: General conclusions

7.1 Functional diversity contributes insight into biodiversity-ecosystem function research

Despite increased responses to biodiversity loss (e.g. protected area coverage), human demand on Earth's ecosystems continue to increase and biodiversity, measured using data such as population trends and extent of habitats, continues to decline (Butchart *et al.*, 2010). It is therefore important to consider how ecosystem processes could be affected by human-mediated biodiversity loss (Hooper *et al.*, 2005). This thesis used birds as a model system to investigate these concepts. 134 birds have gone extinct since 1500 and more than a fifth of extant species are threatened or near-threatened with extinction (IUCN, 2013). Predictions of the number of bird species set to go extinct by the end of this century vary by an order of magnitude; Jetz *et al.* (2007) estimated that 51-80 birds will go extinct by 2100 and an additional 253-456 will become threatened, whereas Şekercioğlu *et al.* (2008) estimated that the most likely scenario involved 400-450 extinctions (up to 2,498 extinctions in the worst case scenario) and 1,770-2,650 additional threatened or near-threatened species. In any event, a number of bird species are projected to go extinct in the next decades due to anthropogenic pressures including habitat loss, climate change and persecution, and these extinctions could impact upon ecosystem processes.

Functional diversity is increasingly being used to investigate the link between biodiversity and ecosystem processes; Cadotte *et al.* (2011) observed that functional diversity is appearing in the literature with increasing frequency and recent publications confirm that this trend is continuing (Figure 7.1). The increase in publications concerning functional diversity approximately coincided with the publication of the Millennium Ecosystem Assessment in 2005, which sought to assess the consequences of biodiversity loss in terms of its impacts on ecosystem services beneficial to human well-being (Millennium Ecosystem Assessment, 2005). Although species richness is generally easier to measure than functional diversity, it is poorly correlated with other aspects of biodiversity including measures of abundance and functional diversity; indeed, when species richness is used as the sole measure of biodiversity it misses nearly 90% of the total diversity using criteria that evaluate composition, taxonomic diversity and functional diversity (Lyashevska & Farnsworth, 2012). The research in this thesis has contributed to the investigation of biodiversity and ecosystem processes by identifying how and why the macroecological distribution of functional diversity of avian assemblages changes in space and time and how functional diversity might change in the future due to species' sensitivities to disturbance and variation in protected area coverage. Previously, functional diversity has been calculated for birds at a country-wide scale (e.g. Great Britain, Petchey *et al.*, 2007; France, Devictor *et al.*, 2010) and has been mapped for other vertebrate taxa at scales up to global coverage (e.g. mammals, Safi *et al.*, 2011; fish, Stuart-Smith *et al.*, 2013), but this is the first study to map a continuous measure of functional diversity for the complete avifauna at a scale that covers more than one continent.

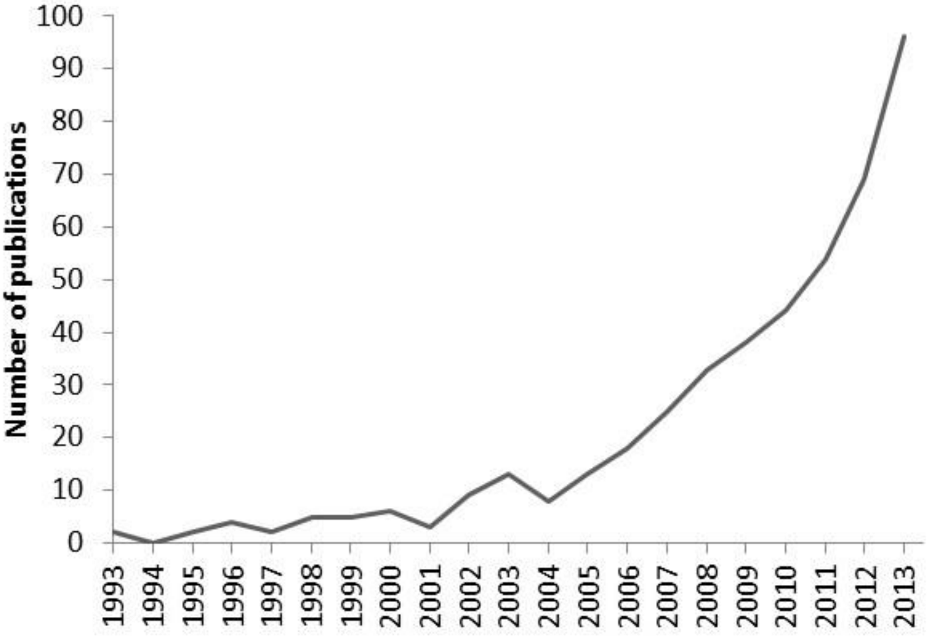

Figure 7.1: The yearly number of publications found using ISI Web of Science using the keywords ‘functional diversity’ and ‘ecology’.

7.2 A signal of environmental filtering is evident in the macroecological distribution of avian functional diversity

Co-occurring species may have similar functional traits that allow adaptation to the local environmental conditions. Consequently environmental filtering can cause trait clustering (Petchey *et al.*, 2007), which may be more evident at large scales (Díaz *et al.*, 1999). In **Chapter three**, functional richness of avian assemblages across the Old World was found to have positive associations with precipitation and temperature, which may signal stronger environmental filtering in very arid or very cold regions. Birds are not the only taxonomic group for which analyses of functional diversity have revealed evidence of environmental filtering; low precipitation was also associated with low functional richness in European fish communities (Schleuter *et al.*, 2012). Furthermore, in **Chapter two**, it was found that the majority of continental interior higher-latitude Palaearctic areas showed greater trait clustering for residents compared to all breeding species; resident species showed greater evidence of being functionally constrained by the seasonally challenging environment at high latitudes.

The association between migratory status and the importance of environmental filtering was further explored by comparing breeding with non-breeding assemblages in the Palaearctic-Afrotropical flyway. In **Chapter four**, it was found that the emigration of species from the high latitudes of the Palaearctic corresponded with a decrease in the volume of functional space occupied during the winter months and that the functional space occupied in the non-breeding season was nested within the functional space occupied in the breeding season. At local scales, the community composition of non-breeding waders in UK estuaries has been found to be consistent with environmental filtering since their traits are under-dispersed (Mendez *et al.*, 2012). Environmental filtering may manifest itself differently for particular functional groups. For example, the low functional richness of terrestrial insectivores during the non-breeding season at high latitudes reflects the lack of available insect prey. Indeed, the range limit of insectivorous bird species wintering in North America is determined more by food availability than physiological constraints (Canterbury, 2002). Additionally, the majority of species that breed above 35° and migrate south for the non-breeding season are insectivorous (Newton, 2008).

7.3 Intra-annual change in community composition and climatic conditions are important factors in the distribution of functional diversity

That environmental filtering is more evident in the non-breeding season is in accordance with other findings in this thesis which indicate that functional diversity changes in space and time as a result of seasonal changes in climatic conditions and community composition. While latitudinal gradients of other biodiversity metrics such as species richness have been found to correlate with energy and habitat heterogeneity (e.g. Evans *et al.*, 2005; Davies *et al.*, 2007a), the findings presented here reveal a greater role of climatic seasonality (e.g. Hurlbert & Haskell, 2003; Carrara & Vázquez, 2010). In **Chapter two**, temperature seasonality had greater explanatory power than mean temperature for functional diversity and temperature seasonality was one of the most important factors explaining SES_{FD}, particularly for resident assemblages. Areas of low seasonality were associated with high SES_{FD} (traits were over-dispersed) for resident assemblages, which also showed evidence of environmental filtering in areas of high seasonality. However, migratory species were relatively unaffected by seasonality and areas of high seasonality were associated with high functional diversity and high SES_{FD} for breeding assemblages.

The restriction of traits for resident species in highly seasonal environments was further explored in **Chapter three**. Areas of high temperature seasonality were associated with a restricted range of aquatic-terrestrial strategies for resident species and were less likely to have birds that use aquatic habitats for foraging. Resident species in these areas were also more likely to be restricted to the more herbivorous region of trait space. Migratory species did not face these restrictions. This was in agreement with the findings presented in **Chapter four** that terrestrial herbivores were the functional group with the lowest proportion of migratory behaviour and that there was extremely low functional richness of aquatic foragers at high latitudes in the non-breeding season. The findings that seasonality restricts the traits of sedentary species, but not migratory species, is corroborated by the observation that the timing of water birds' migration is related to freeze-up and that the majority of species that breed at high latitudes and migrate to lower latitudes during the winter months are insectivorous (Newton, 2008).

Moreover, in **Chapter four**, it was found that migratory species make important contributions to functional diversity in their breeding and wintering areas and that there are therefore considerable intra-annual changes in the distribution of functional diversity. However, many migratory species may be more sensitive to human-mediated disturbance since they are showing considerable population declines (Sanderson *et al.*, 2006). In **Chapter five**, it was found that full and partial migrants or nomads were more sensitive to local human disturbance than sedentary species and that global extinction risk for range-restricted species of South and South-east Asia was higher for migratory species. The decline of migratory species could therefore have important consequences for functional diversity and associated ecosystem processes.

7.4 The effects of extinctions on ecosystem processes depend on which species go extinct and their associated traits

The effects of species extinctions on ecosystem processes will depend in part on the degree of redundancy in communities; the loss of some species may not be as ecologically damaging as others if they have functional analogues with which they co-exist (Ehrlich & Ehrlich, 1981; Walker, 1992). Analyses in **Chapter two** and **Chapter three** indicated that bird assemblages show redundancy at high species richness whether functional diversity is measured using a dendrogram or as the convex hull of species in multidimensional trait space. This suggests that species-rich regions could absorb some avian extinctions without the loss of their associated ecosystem services. Redundancy was much more evident when functional diversity was measured as the volume of multidimensional functional space occupied (functional richness). Compared to dendrogram-based measures of functional diversity, trait values at the extremes of occupied trait space have a greater influence on functional richness. Therefore, the effects of species loss on ecosystem processes may depend in part on whether species with extreme trait values are relatively more important for the maintenance of these processes.

Some species that face threatening processes might be more likely to go extinct because their traits make them more vulnerable. The traits identified as being associated with sensitivity in **Chapter five** can be termed ‘functional response traits’ since they determine how species respond to environmental disturbance (Hooper *et al.*, 2005). Species were particularly vulnerable if they were highly forest dependent and/or had a narrow habitat breadth. The loss of functional diversity and reduced delivery of associated ecosystem services will depend on the correlation between these traits and ‘functional effect traits’, which affect ecosystem function (Hooper *et al.*, 2005). If habitat specialists are also keystone species for particular ecosystem processes, then these processes could also be highly vulnerable.

7.5 Functional diversity can be used as a means of prioritising conservation

Since the cost of protecting all species and habitats outstrips the resources available for conservation, different ways of prioritising regions for conservation have been suggested such as Myers’ (2000) hotspots of endemism and habitat loss. Given that functional diversity is associated with ecosystem processes (Cadotte *et al.*, 2011), including ecosystem services vital to human well-being that are also of great economic importance (Costanza *et al.*, 1998), prioritising conservation to optimise functional diversity could ensure continued delivery of these services. In **Chapter four**, it was shown that the distribution of functional diversity changes considerably between seasons, and therefore for birds – and other taxa which show significant seasonal distributional changes – the identification of sites important for conservation should recognise that sites may vary in their relative importance for biodiversity between seasons. In **Chapter six**, it was shown that species with the smallest range sizes, which are less likely to be covered by the global protected area network (Rodrigues *et al.*, 2004b), have significantly different traits from widespread, better protected species. Indeed, species that fall in the 'gaps' between protected areas were more likely to be canopy-dwelling, small-bodied herbivores. Since canopy species must by definition inhabit forests, these gap species may also share the traits associated with sensitivity identified in **Chapter five** as being forest-dependency and narrow habitat breath. These species may provide important services such as seed dispersal and pollination (Şekercioğlu, 2006). Therefore, new protected areas could be sited so that these traits are protected.

7.6 Some methodological considerations addressed in the analysis of data for this thesis

Petchey and Gaston (2006) identified a series of questions to be addressed in studies measuring functional diversity. In order to use appropriate functional traits, they suggest that researchers must ask: (1) What types of traits?; (2) Which traits?; (3) How many traits?; and authors must decide how to go about (4) obtaining trait values.

The types of traits chosen in this study were those relating to resource use for two reasons since many ecosystem processes to which birds contribute are related to their foraging ecology and this also represents an approach used for measuring avian functional diversity by other researchers (e.g. Petchey et al., 2007). Şekercioğlu (2006) suggested that the most influential ecological function performed by birds is seed dispersal; approximately 3,150 frugivorous bird species contribute to this service to some degree. Additionally, many nectarivorous bird species pollinate the plants that they visit while they forage, birds that feed on invertebrates and vertebrates can contribute to pest control directly through consumption or by indirectly limiting pest activity through fear and scavengers provide sanitary services such as carcass and waste disposal.

Therefore, information on species' trophic level was provided using six binary traits related to different diets (Table 2.1). Body mass was included as a proxy for the quantity and size of resources consumed. For example, the Rufous-necked Hornbill (*Aceros nipalensis*) and the Crimson-breasted Flowerpecker (*Prionochilus percussus*) are both frugivorous species that occur in Indo-Malaya and therefore may be contributing to seed dispersal in this region. However since the former may be about 2.5kg and the latter less than 10g, they will be consuming fruits, and therefore dispersing seeds, from different plant species. The group size in which species most commonly forage can also affect the quantity of resources consumed; species that join mixed-species flocks forage at a higher rate in flocks than when foraging alone (Sridhar *et al.*, 2009). Circadian activity was included as it determines not only when resources are consumed, but in some cases also what resources are consumed. For instance, diurnal birds of prey are more likely to catch diurnal prey and vice versa for nocturnal birds of prey. The habitat strata used and the foraging locations determine where resources are accessed. For example, aerial insectivores that are active at the canopy level or higher will be accessing different insect prey than species that forage on vegetation in the shrub layer/understorey.

Petchey and Gaston (2006) state that when choosing traits, researchers should include "*all traits that are important for the function of interest and no traits that are functionally uninformative*". This needs to be kept in mind when choosing the number of traits to include. The fewer traits that are included, the greater the apparent redundancy of the assemblages (Petchey & Gaston, 2006). The effects of including fewer traits from my dataset are explored in Appendix S10: Some methodological considerations addressed in the analysis of data for this thesis. As expected, using only one trait led to functional diversity saturating at very low species richness, but with the addition of traits this redundancy became less apparent.

The process of obtaining the trait data for the analyses of this thesis has involved the collation of traits from 115 references (Appendix S1). Where possible, body mass data were used that averaged values from several individuals. In each analysis, >90% of the species-trait combinations represented data collated for individual species. Inevitably, it was impossible to collate data on all traits for all species and so genus – or, failing that, family – values were used in place of missing trait data. The effects of using higher taxonomic values for a subset of the data are explored in Appendix S10: Some methodological considerations addressed in the analysis of data for this thesis. The substitution of specific data for genus or family values had only a small effect on the results obtained; even when only 75% of the data were true species values the correlations with the true values of functional diversity (measured using PCoA position and functional richness) exceeded 0.9 in all cases.

7.7 Future directions

At the start of this thesis, it was stated that birds were a very suitable model system for these analyses because they are well-studied and because they contribute important ecosystem services (Şekercioğlu, 2006), which may be at risk as a result of biodiversity loss (Şekercioğlu *et al.*, 2004). Some of the ecosystem services provided by birds may also be provided by members of other taxonomic groups, e.g. birds and mammals both disperse seeds of a wide variety of plant species; more than half of the tree species in tropical forests produce fleshy fruits that birds or mammals consume (Howe & Smallwood, 1982). It would therefore be interesting to investigate whether there are complementary patterns of functional diversity of different higher taxonomic groups providing similar services, i.e. is there higher functional diversity of mammalian seed dispersers where there is lower functional diversity of avian seed dispersers?

The analyses in this thesis have been made possible by the provision of a complete set of Extent of Occurrence (EOO) maps for all global birds by BirdLife International (Birdlife International & Natureserve, 2011). Since species do not have a homogenous distribution within the outermost limits of their geographic range, their Area of Occupancy (AOO) is consistently smaller than their EOO (Gaston, 2003). Such commission errors (where a species is recorded as being present in an area in which it is not) can cause errors such incorrectly identifying the drivers of diversity patterns (Hurlbert & Jetz, 2007) or poor choices in prioritising conservation efforts (Rondinini *et al.*, 2006). Some of the analyses in this thesis, particularly those in chapter six regarding range size, could therefore be refined by the use of Extent of Suitable Habitat (ESH) maps. For example, ESH estimates of species richness of terrestrial mammals is approximately one-third lower than that estimated using EOO maps (Rondinini *et al.*, 2011). A gap analysis using ESH maps would indicate that the global protected area network is less effective than suggested by analyses using EOO maps. This refinement could therefore improve the identification of priority sites for conservation and increase the impact of this research.

Appendices

Appendix S1: Sources used for bird trait data

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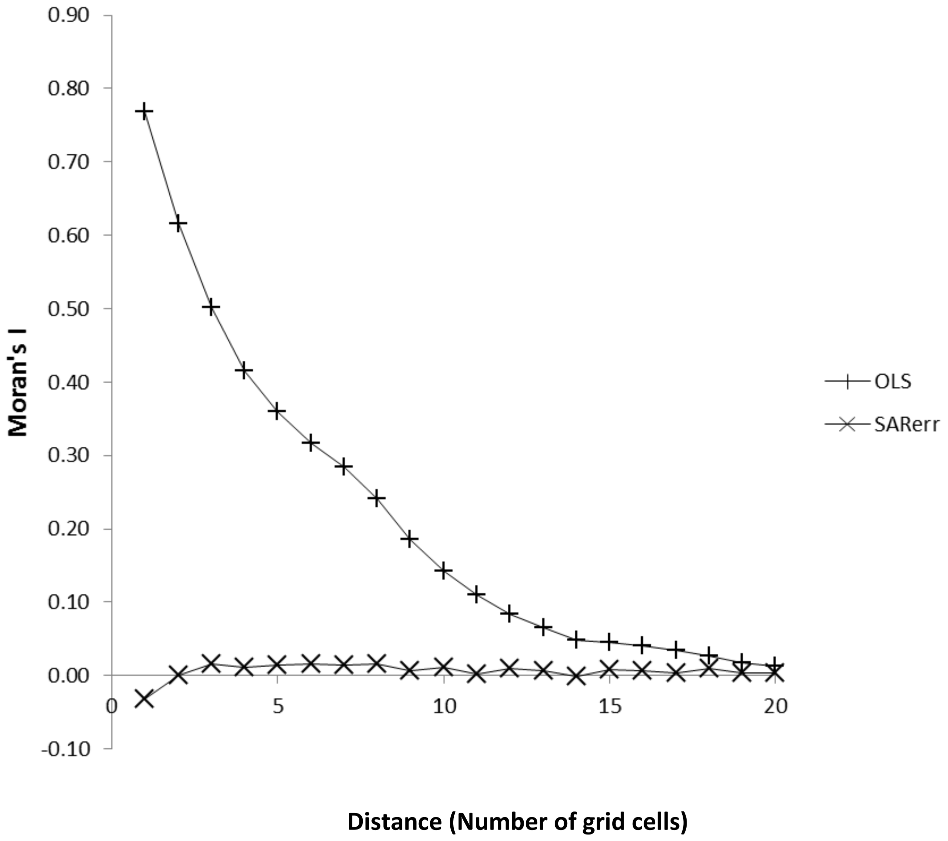
Appendix S2: Further information on data used for environmental and anthropogenic drivers in chapters two and three

To calculate climate change velocity, we used ocean–atmosphere general circulation model (GCM) 'snap-shot' simulations for 21,000 BP and the present (Singarayer & Valdes, 2010) in order to calculate the change in temperature and rainfall between these periods. The raw resolution of the climate model is 3.75°x2.5° and was bi-linearly interpolated onto a 1° grid. Although climate model simulations are not a perfect representation of the changes over the last 21,000 years, they do provide a global reconstruction of change over this period. The results of the model simulation have been compared to observational data to confirm that the broad patterns of change are well represented (Singarayer & Valdes, 2010). We used the 2.5′ WorldClim climate data (Hijmans *et al.*, 2005) to calculate the spatial gradient in temperature and precipitation. Spatial gradients were calculated as the maximum difference value between the focal cell and each cell of the 3 x 3 grid cell neighbourhood. This difference was standardized by distance (i.e. divided by distance corrected for decrease in cell width with increase in latitude). To eliminate the incidence of flat (zero) spatial gradients resulting in velocity estimates of infinity, we added 0.001 to each pixel for temperature and precipitation.

We made our consideration of contemporary versus historic variables as robust as possible by using available historical data rather than contemporary surrogates to represent historical gradients of past climate or human effects, and by avoiding variables that may be considered at different temporal scales, e.g. elevation range. Topographic variability has changed little since the Last Glacial Maximum (LGM) and so could reflect the influence of processes occurring over either historic or contemporary timescales or both (e.g. Schuldt & Assmann, 2009). We regard the inclusion of our climate velocity predictors as better capturing the historical components of topographic gradients as they interact with climate change. It could also be argued that certain predictors we use to represent contemporary gradients, such as contemporary climate seasonality, are indeed surrogates of historical gradients if we assume that contemporary patterns of seasonality are spatially congruent with past patterns. However, evidence suggests that differences in past and present climate not only when comparing mean climate but also levels of climate seasonality, e.g. temperature seasonality in New Zealand is higher now than in the LGM and this is reflected in the change in distribution of vegetation types (Drost *et al.*, 2007).

Appendix S3: Accounting for spatial autocorrelation



Supplementary Figure 1: Spatial correlogram showing Moran's I for the residuals of the MAM of SES_{FD} across the Old World for the OLS regression and the simultaneous autoregressive model (SAR_{err}).

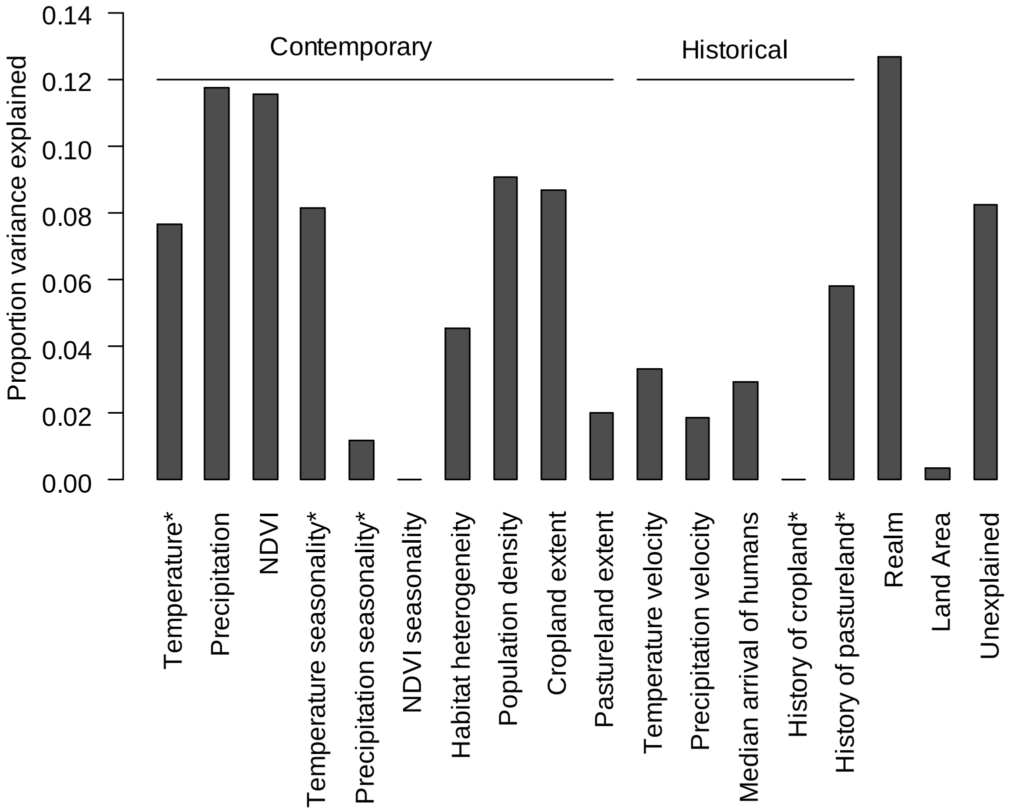
Appendix S4: Analyses of species richness and functional diversity using an Old World regional pool

Supplementary Table 1: Single-predictor models of species richness for all breeding species. All models also include realm and land area. Models either include just a linear term (L) or a linear and a quadratic term (LQ). The r^2 is determined by hierarchical partitioning. Significance values: ** <0.0001, *** <0.001, ** <0.01, * <0.05, NS Non-significant**

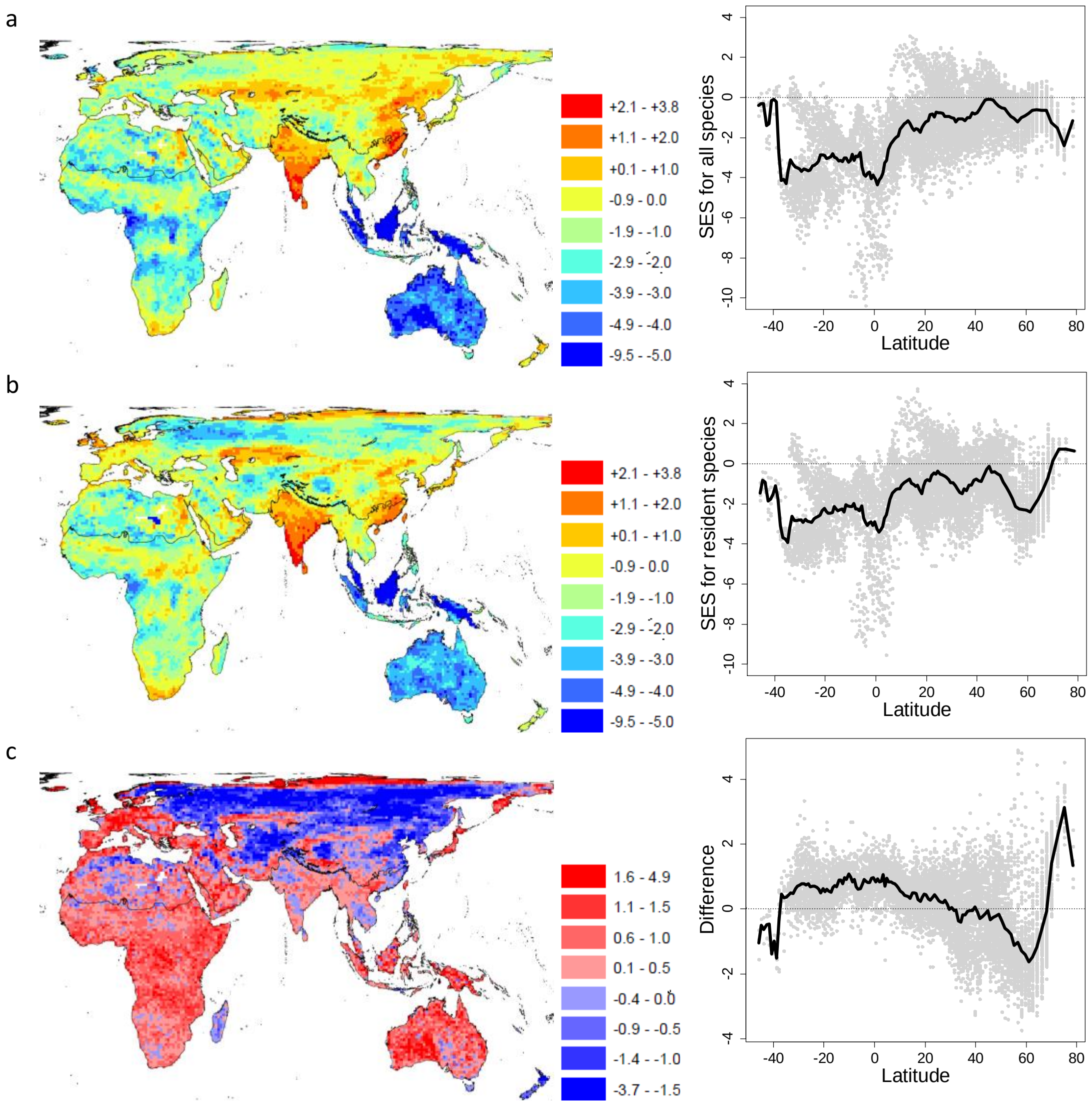
	Variable	Terms	AIC (rank)	r^2	Parameter (±SE)	
Contemporary	**Mean annual temperature**	L	83741	0.06	-7.23	(±1.71)****
		LQ	83254 (1)	0.50	+26.55	(±2.25)****
					-37.11	(±1.66)****
	Total annual precipitation	L	83405 (3)	0.45	+19.26	(±1.01)****
	Mean annual NDVI	L	83258 (2)	0.48	+17.34	(±0.76)****
	Temperature seasonality	L	83725	0.38	-16.51	(±2.80)****
		LQ	83617 (9)	0.46	-80.17	(±6.64)****
					+50.56	(±4.80)****
	Precipitation seasonality	L	83749	0.03	-3.58	(±1.10)**
		LQ	83748 (15)	0.03	+0.03	(±2.69) NS
					-3.70	(±2.51) NS
	NDVI seasonality	L	83679 (11)	0.09	+6.04	(±0.68)****
	Habitat heterogeneity	L	83432 (5)	0.15	+6.32	(±0.35)****
	Human population density in 2000AD	L	83645 (10)	0.11	+4.41	(±0.41)****
	Cropland extent in 2000AD	L	83600 (8)	0.18	+5.88	(±0.46)****
	Pastureland extent in 2000AD	L	83716 (13)	0.07	+3.57	(±0.54)****
Historical	**Temperature change velocity since LGM**	L	83426 (4)	0.20	-7.13	(±0.39)****
	Precipitation change velocity since LGM	L	83560 (7)	0.11	-5.16	(±0.36)****
	Median arrival time of humans	L	83532 (6)	0.02	+2.87	(±0.80)***
	Period since conversion to cropland	L	83705 (12)	0.64	+2.85	(±0.38)****
		LQ	83705	0.05	+1.71	(±1.16) NS
					+1.38	(±1.34) NS
	Period since conversion to pastureland	L	83721 (14)	0.02	+3.28	(±0.53)****
		LQ	83722	0.02	+2.95	(±1.23)*
					+0.44	(±1.48) NS

Supplementary Table 2: Summary of minimum adequate model for predictors of species richness. Significance values: **<0.0001, ***<0.001, **<0.01, *<0.05, NS Non-significant. [a] Zero by default.**

	Variable	Parameter estimate (±SE)	
Contemporary	Mean temperature	+34.43	(±2.46)****
	Mean temperature²	-29.00	(±1.67)****
	Total precipitation	+9.48	(±1.11)****
	Mean NDVI	+8.09	(±0.82)****
	Temperature seasonality	-38.30	(±6.50)****
	Temperature seasonality²	+33.68	(±4.64)****
	Precipitation seasonality	+3.70	(±2.53) NS
	Precipitation seasonality²	-5.09	(±2.35)*
	Habitat heterogeneity	+3.61	(±0.36)****
	Human population density in 2000AD	+1.97	(±0.42)****
	Cropland extent in 2000AD	+2.53	(±0.48)****
	Pastureland extent in 2000AD	+1.99	(±0.56)***
Historical	Temperature change velocity since LGM	-4.44	(±0.48)****
	Precipitation change velocity since LGM	-2.48	(±0.38)****
	Median arrival time of humans	+1.17	(±0.74) NS
	Period since conversion to pastureland	-1.60	(±1.22) NS
	Period since conversion to pastureland²	+4.35	(±1.40)**
Covariates	Realm: Afrotropics	0[a]	
	Realm: Australasia	-49.58	(±12.65)****
	Realm: Indo-Malaya	+17.86	(±3.75)****
	Realm: Palaearctic	-4.20	(±2.48) NS
	Land area	+2.45	(±0.18)****
	r²	0.92	



Supplementary Figure 2: The relative importance of predictors as determined by hierarchical partitioning in the final models for species richness.

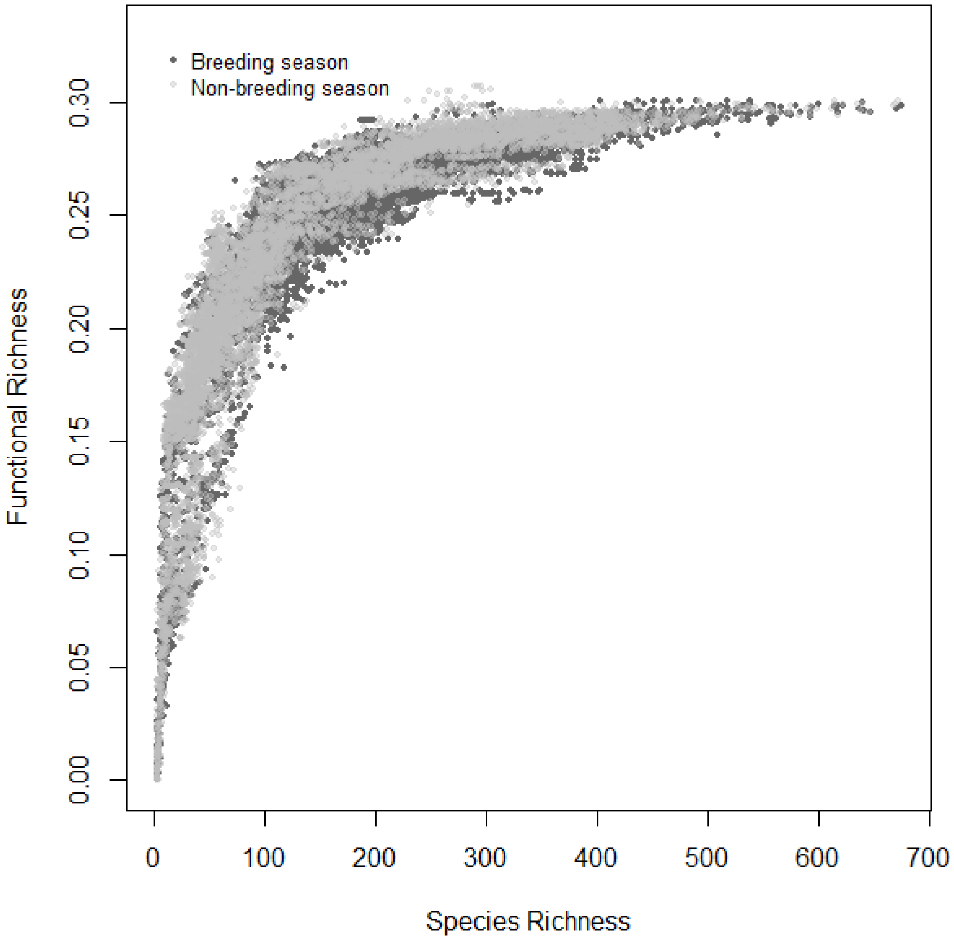


Supplementary Figure 3: The distribution of Standardised Effect Size of Functional Diversity (SES_{FD}) for (a) all breeding species and (b) resident species, and (c) the difference between SES_{FD} of residents and all breeding species. These were calculated using a regional pool of all Old World species. Red areas are where SES_{FD} is higher for resident species than for all breeding species. Plots show the latitudinal trends: grey points are individual grid cell values and black lines are latitudinal mean values.

Supplementary Table 3: Summary of minimum adequate models for predictors of FD_{obs} and SES_{FD} calculated with a regional pool of all Old World species. Significance values: **<0.0001, ***<0.001, **<0.01, *<0.05, NS Non-significant. [a] Zero by default.**

		Parameter estimate (±SE)		
	Variable	**FD_{obs} All breeding species**	**SES_{FD} All breeding species**	**SES_{FD} Residents only**
Contemporary	**Mean temperature**	+0.018 (±0.001)****	-0.22 (±0.08)**	-0.21 (±0.08)*
	Mean temperature^2	-0.012 (±0.001)****	+0.29 (±0.06)****	+0.27 (±0.06)****
	Total precipitation	+0.004 (±0.001)****	-	-
	Mean NDVI	+0.004 (±0.000)****	-	-0.14 (±0.03)****
	Temperature seasonality	-0.018 (±0.003)****	+0.60 (±0.07)****	+0.40 (±0.18)*
	Temperature seasonality^2	+0.019 (±0.002)****	-	-0.67 (±0.14)****
	Precipitation seasonality	+0.003 (±0.001)*	+0.29 (±0.09)**	-0.06 (±0.04) NS
	Precipitation seasonality^2	-0.003 (±0.001)*	-0.20 (±0.08)*	-
	NDVI seasonality	+0.001 (±0.000)*	-	-
	Habitat heterogeneity	+0.002 (±0.000)****	-	-
	Human population density in 2000AD	+0.001 (±0.000)****	-	-
	Cropland extent in 2000AD	+0.001 (±0.000)****	-	-
	Pastureland extent in 2000AD	+0.001 (±0.000)***	-0.05 (±0.02)*	-
Historical	**Temperature change velocity since LGM**	-0.002 (±0.000)****	+0.06 (±0.02)***	+0.06 (±0.02)***
	Precipitation change velocity since LGM	-0.001 (±0.000)****	+0.03 (±0.01) NS	-
	Median arrival time of humans	-	-0.01 (±0.03) NS	-0.15 (±0.03)****
	Period since conversion to cropland	-0.001 (±0.001)*	-	-0.10 (±0.04)*
	Period since conversion to cropland^2	+0.002 (±0.001)**	-	+0.12 (±0.05)*
	Period since conversion to pastureland	+0.000 (±0.001) NS	+0.09 (±0.05)*	+0.05 (±0.04) NS
	Period since conversion to pastureland^2	+0.001 (±0.001) NS	-0.09 (±0.05) NS	-0.14 (±0.05)**
Covariates	**Realm: Afrotropics**	0[a]	0[a]	0[a]
	Realm: Australasia	-0.016 (±0.007)*	-1.44 (±0.20)****	-2.20 (±0.22)****
	Realm: Indo-Malaya	+0.006 (±0.002)**	+0.47 (±0.13)***	+0.28 (±0.13)*
	Realm: Palaearctic	-0.005 (±0.001)***	-0.11 (±0.09) NS	+0.01 (±0.09) NS
	Land area	+0.001 (±0.000)****	-0.02 (±0.01)***	-0.05 (±0.01)****
	r^2	0.90	0.71	0.61

Appendix S5: Analyses of functional richness and PCoA dimensions



Supplementary Figure 4: The relationship between species richness and functional richness in the breeding and non-breeding seasons.

Univariate models suggested that contemporary climate was most important for predicting functional richness. The best-fitting predictor for the functional richness of all species present in the breeding season was temperature seasonality, followed by mean precipitation; areas of high temperature seasonality and high precipitation were associated with higher functional richness (Supplementary Table 4). For resident species, the best-fitting predictor was mean temperature; higher temperatures were associated with higher functional richness. The second best fit predictor was temperature seasonality. In contrast to the model for all species, areas of high temperature seasonality were associated with lower functional richness (Supplementary Table 4).

Supplementary Table 4: AIC values (and rank) and parameter estimates (±SE) for univariate models for functional richness for all species and residents only. All models also include species richness, species richness², realm and land area. Significance values: ** < 0.0001, *** <0.001, ** <0.01, * <0.05, NS Non-significant**

Variable	All species			Residents		
Mean temperature	-59603 (7)	+0.0042 (±0.0043)	NS	-53560 (1)	+0.0548 (±0.0050)	****
Mean precipitation	-59625 (2)	+0.0295 (±0.0060)	****	-53474 (5)	+0.0286 (±0.0079)	***
Mean NDVI	-59320 (15)	-0.0019 (±0.0023)	NS	-53483 (3)	-0.0009 (±0.0031)	NS
Temperature seasonality	-59626 (1)	+0.0328 (±0.0065)	****	-53491 (2)	-0.0473 (±0.0076)	****
Precipitation seasonality	-59602 (8=)	+0.0013 (±0.0043)	NS	-53466 (8)	+0.0132 (±0.0057)	*
NDVI seasonality	-59321 (14)	+0.0050 (±0.0020)	*	-53480 (4)	+0.0056 (±0.0027)	*
Number of landcover types	-59602 (10)	-0.0013 (±0.0015)	NS	-53462 (10)	-0.0022 (±0.0020)	NS
Human population density in 2000AD	-59604 (6)	+0.0017 (±0.0012)	NS	-53461 (11)	+0.0015 (±0.0016)	NS
Cropland extent in 2000AD	-59598 (11=)	+0.0008 (±0.0015)	NS	-53460 (12)	+0.0043 (±0.0020)	*
Grassland extent in 2000AD	-59598 (11=)	+0.0008 (±0.0012)	NS	-53456 (14)	-0.0004 (±0.0016)	NS
Temperature change velocity since LGM	-59602 (8=)	+0.0008 (0.0017)	NS	-53472 (6)	-0.0075 (±0.0023)	***
Precipitation change velocity since LGM	-59605 (5)	+0.0048 (±0.0025)	NS	-53464 (9)	-0.0060 (±0.0034)	NS
Median arrival of humans	-59456 (13)	+0.0033 (±0.0022)	NS	-53326 (15)	-0.0044 (±0.0030)	NS
Duration of cropland	-59607 (3)	+0.0029 (±0.0010)	**	-53468 (7)	+0.0045 (±0.0013)	***
Duration of grassland	-59606 (4)	+0.0035 (0.0012)	**	-53458 (13)	+0.0025 (±0.0016)	NS

Supplementary Table 5: AIC values (and rank) and parameter estimates (±SE) for univariate models for mean PCoA dimension scores for all species and residents only. All models also include realm and land area. Significance values: ** < 0.0001, *** <0.001, ** <0.01, * <0.05, NS Non-significant**

Variable	Dimension one						Dimension two						Dimension three						Dimension four					
	All species			Residents			All species			Residents			All species			Residents			All species			Residents		
Temp	-64677 (12)	-0.0036 (±0.0037)	NS	-62004 (13)	+0.0012 (±0.0042)	NS	-63497 (5)	-0.0075 (±0.0037)	*	-59153 (11)	-0.0008 (±0.0045)	NS	-62027 (1)	+0.0249 (±0.0036)	****	-57214 (4)	+0.0374 (±0.0045)	****	-70853 (7=)	+0.0073 (±0.0026)	**	-66678 (11)	+0.0028 (±0.0031)	NS
Prec	-64893 (1)	-0.0746 (±0.0049)	****	-62111 (3)	-0.0608 (±0.0056)	****	-63597 (2)	-0.0519 (±0.0051)	****	-59238 (4)	-0.0567 (±0.0061)	****	-61995 (2)	+0.0192 (±0.0049)	****	-57149 (10=)	+0.0074 (±0.0063)	NS	-70868 (2)	-0.0167 (±0.0034)	****	-66726 (4)	-0.0293 (±0.0042)	****
NDVI	-64383 (14)	-0.0247 (±0.0018)	****	-62320 (1)	-0.0188 (±0.0020)	****	-63096 (15)	-0.0186 (±0.0019)	****	-59859 (2)	-0.0222 (±0.0022)	****	-61644 (14)	+0.0029 (±0.0020)	NS	-58110 (1)	-0.0068 (±0.0024)	**	-70517 (14)	-0.0078 (±0.0013)	****	-66657 (14)	-0.0152 (±0.0016)	****
TempSea	-64740 (3)	-0.0557 (±0.0067)	****	-62011 (8)	-0.0200 (±0.0075)	**	-63685 (1)	-0.1043 (±0.0069)	****	-59505 (3)	-0.1332 (±0.0070)	****	-61992 (3)	-0.0189 (±0.0055)	***	-57222 (3)	-0.0590 (±0.0063)	****	-70866 (3)	-0.0210 (±0.0043)	****	-66785 (1)	-0.0609 (±0.0055)	****
PrecSea	-64685 (8)	+0.0105 (±0.0036)	**	-62018 (7)	+0.0154 (±0.0041)	***	-63494 (10)	-0.0013 (±0.0037)	NS	-59155 (6=)	+0.0067 (±0.0046)	NS	-61984 (7)	+0.0068 (±0.0038)	NS	-57148 (12=)	+0.0034 (±0.0049)	NS	-70847 (11)	+0.0035 (±0.0026)	NS	-66677 (12)	0.0000 (±0.0031)	NS
NDVISea	-64300 (15)	-0.0157 (±0.0016)	****	-62310 (2)	-0.0151 (±0.0017)	****	-63144 (14)	-0.0203 (±0.0017)	****	-60098 (1)	-0.0355 (±0.0019)	****	-61638 (15)	+0.0024 (±0.0018)	NS	-58084 (2)	-0.0008 (±0.0021)	NS	-70496 (15)	-0.0058 (±0.0011)	****	-66740 (3)	-0.0160 (±0.0014)	****
Hab	-64709 (5)	-0.0064 (±0.0011)	****	-62024 (6)	-0.0057 (±0.0013)	****	-63496 (6)	-0.0019 (±0.0012)	NS	-59155 (6=)	-0.0025 (±0.0015)	NS	-61982 (9)	-0.0017 (±0.0013)	NS	-57153 (7=)	-0.0035 (±0.0017)	*	-70863 (5)	-0.0035 (±0.0008)	****	-66701 (5)	-0.0050 (±0.0010)	****
PopDens	-64682 (10)	-0.0022 (±0.0009)	*	-62005 (11=)	-0.0011 (±0.0011)	NS	-63496 (7)	-0.0015 (0.0010)	NS	-59154 (10)	-0.0014 (±0.0012)	NS	-61983 (8)	+0.0018 (±0.0011)	NS	-57149 (10=)	+0.0011 (±0.0014)	NS	-70852 (10_	-0.0018 (±0.0007)	**	-66687 (8)	-0.0027 (±0.0008)	**
CropEx	-64683 (9)	+0.0030 (±0.0012)	*	-62004 (14)	+0.0013 (±0.0013)	NS	-63495 (8=)	+0.0037 (±0.0012)	**	-59151 (12)	+0.0038 (±0.0015)	*	-61990 (5)	+0.0055 (±0.0013)	****	-57153 (7=)	+0.0059 (±0.0017)	***	-70853 (7=)	+0.0029 (±0.0009)	***	-66682 (10)	+0.0031 (±0.0011)	**
GrassEx	-64678 (11)	+0.0012 (±0.0009)	NS	-62005 (11=)	+0.0018 (±0.0011)	NS	-63486 (12)	-0.0001 (±0.0010)	NS	-59145 (13=)	+0.0003 (±0.0012)	NS	-61975 (11)	-0.0013 (±0.0011)	NS	-57142 (14)	-0.0006 (±0.0014)	NS	-70845 (12)	-0.0011 (±0.0007)	NS	-66675 (13)	-0.0010 (±0.0008)	NS
TempVel	-64823 (2)	+0.0155 (±0.0013)	****	-62042 (5)	+0.0091 (±0.0015)	****	-63562 (3)	+0.0113 (±0.0014)	****	-59161 (5)	+0.0051 (±0.0017)	**	-61988 (6)	+0.0041 (±0.0015)	**	-57175 (5)	+0.0099 (±0.0019)	****	-70902 (1)	+0.0071 (±0.0009)	****	-66754 (2)	+0.0103 (±0.0012)	****
PrecVel	-64703 (6)	+0.0099 (±0.0019)	****	-62006 (10)	+0.0030 (±0.0022)	NS	-63529 (4)	+0.0122 (±0.0020)	****	-59155 (6=)	+0.0038 (±0.0026)	NS	-61991 (4)	+0.0072 (±0.0022)	**	-57169 (6)	+0.0130 (±0.0028)	****	-70864 (4)	+0.0062 (±0.0014)	****	-66699 (6)	+0.0081 (±0.0017)	****
HumArr	-64568 (13)	-0.0112 (±0.0017)	****	-61869 (15)	-0.0063 (±0.0020)	**	-63339 (13)	-0.0017 (±0.0018)	NS	-59008 (15)	+0.0024 (±0.0023)	NS	-61826 (13)	-0.0008 (±0.0019)	NS	-57022 (15)	-0.0104 (±0.0025)	****	-70722 (13)	-0.0087 (±0.0013)	****	-66640 (15)	-0.0176 (±0.0015)	****
CropHist	-64739 (4)	-0.0057 (±0.0007)	****	-62045 (4)	-0.0054 (±0.0008)	****	-63493 (11)	-0.0021 (±0.0008)	**	-59145 (13=)	-0.0002 (±0.0010)	NS	-61977 (10)	+0.0014 (±0.0008)	NS	-57148 (12=)	+0.0027 (±0.0011)	*	-70853 (7=)	-0.0018 (±0.0005)	***	-66686 (9)	-0.0024 (±0.0007)	***
GrassHist	-64690 (7)	-0.0035 (±0.0009)	***	-62008 (9)	-0.0025 (±0.0011)	*	-63495 (8=)	-0.0030 (±0.0010)	**	-59155 (6=)	-0.0040 (±0.0013)	**	-61974 (12)	+0.0009 (±0.0011)	NS	-57153 (7=)	-0.0047 (±0.0014)	***	-70858 (6)	-0.0027 (±0.0007)	****	-66692 (7)	-0.0037 (±0.0009)	****

Supplementary Table 6: AIC values (and rank) and parameter estimates (±SE) for univariate models for the range of PCoA dimension scores for all species and residents only. All models also include species richness, species richness^2, realm and land area. Significance values: ** < 0.0001, *** <0.001, ** <0.01, * <0.05, NS Non-significant**

Variable	Dimension one						Dimension two						Dimension three						Dimension four					
	All species			Residents			All species			Residents			All species			Residents			All species			Residents		
Temp	-2130.5	+0.2961	***	-35131	+0.1093	****	3402.3	-0.2002	*	-37517	+0.0368	**	343.41	-0.9283	****	-43825	-0.0051	NS	703.50	+0.0299	NS	-43947	+0.0756	****
	(2)	(±0.0815)		(3)	(±0.0131)		(8)	(±0.0991)		(2)	(±0.0118)		(3)	(±0.0830)		(10=)	(±0.0087)		(10)	(±0.0961)		(3)	(±0.0094)	
Prec	-2140.1	+0.5629	****	-35074	+0.0585	**	3405.5	-0.0165	NS	-37509	-0.0256	NS	403.98	+0.5344	****	-43857	+0.0725	****	703.41	+0.0574	NS	-43906	+0.0440	**
	(1)	(±0.1142)		(4=)	(±0.0201)		(15)	(±0.1460)		(5=)	(±0.0177)		(4)	(±0.1290)		(3)	(±0.0128)		(9)	(±0.1350)		(4)	(±0.0139)	
NDVI	-2097.0	+0.0575	NS	-35579	+0.0104	NS	3404.2	+0.0671	NS	-37243	-0.0291	****	316.75	-0.0752	NS	-43884	+0.0098	NS	754.06	-0.0687	NS	-44044	+0.0135	**
	(15)	(±0.0436)		(2)	(±0.0078)		(10)	(±0.0571)		(14)	(±0.0071)		(1)	(±0.0492)		(1)	(±0.0051)		(14)	(±0.0506)		(2)	(±0.0051)	
TempSea	-2117.3	+0.0188	NS	-35066	+0.0106	NS	3343.5	+1.2375	****	-37549	-0.1118	****	420.62	+0.0291	NS	-43837	+0.0456	***	660.78	-1.0407	****	-43896	+0.0035	NS
	(11=)	(±0.1329)		(8=)	(±0.0203)		(1)	(±0.1372)		(1)	(±0.0172)		(11)	(±0.1457)		(4)	(±0.0128)		(1)	(±0.1562)		(8=)	(±0.0161)	
PrecSea	-2117.4	+0.0289	NS	-35066	+0.0050	NS	3402.5	+0.1829	NS	-37509	+0.0168	NS	420.04	+0.0727	NS	-43833	+0.0274	**	702.51	-0.1007	NS	-43896	+0.0005	NS
	(10)	(±0.0826)		(8=)	(±0.0145)		(9)	(±0.1053)		(5=)	(±0.0127)		(9)	(±0.0932)		(5)	(±0.0092)		(6)	(±0.0965)		(8=)	(±0.0100)	
NDVISea	-2122.2	+0.1429	***	-35607	+0.0378	****	3399.9	+0.1323	**	-37230	-0.0218	***	320.64	+0.0241	NS	-43876	+0.0113	*	758.87	-0.0144	NS	-44164	+0.0458	****
	(3)	(±0.0377)		(1)	(±0.0067)		(5)	(±0.0494)		(15)	(±0.0061)		(2)	(±0.0426)		(2)	(±0.0044)		(15)	(±0.0438)		(1)	(±0.0044)	
Hab	-2119.2	-0.0379	NS	-35066	+0.0005	NS	3400.6	+0.0809	*	-37508	-0.0045	NS	418.97	+0.0408	NS	-43825	-0.0024	NS	703.59	+0.0004	NS	-43898	-0.0042	NS
	(6)	(±0.0276)		(8=)	(±0.0052)		(6)	(±0.0367)		(7=)	(±0.0046)		(7)	(±0.0314)		(10=)	(±0.0034)		(12=)	(±0.0318)		(7)	(±0.0033)	
PopDens	-2118.0	+0.0188	NS	-35069	+0.0078	NS	3401.2	+0.0622	*	-37507	+0.0018	NS	420.64	-0.0016	NS	-43832	+0.0073	**	703.52	+0.0068	NS	-43896	-0.0005	NS
	(7=)	(±0.0225)		(7)	(±0.0042)		(7)	(±0.0299)		(10)	(±0.0038)		(12)	(±0.0256)		(6=)	(±0.0027)		(11)	(±0.0259)		(10)	(±0.0027)	
CropEx	-2119.4	+0.0379	NS	-35061	+0.0032	NS	3405.2	+0.0130	NS	-37508	+0.0112	*	407.16	-0.1220	***	-43821	-0.0047	NS	698.70	+0.0675	*	-43895	+0.0056	NS
	(5)	(±0.0280)		(13=)	(±0.0053)		(14)	(±0.0371)		(7=)	(±0.0046)		(5)	(±0.0318)		(12)	(±0.0034)		(3)	(±0.0322)		(11)	(±0.0034)	
GrassEx	-2118.0	+0.0148	NS	-35063	+0.0055	NS	3405.0	+0.0180	NS	-37503	+0.0014	NS	421.15	-0.0212	NS	-43820	-0.0028	NS	702.94	-0.0099	NS	-43893	-0.0022	NS
	(7=)	(±0.0224)		(12)	(±0.0042)		(12=)	(±0.0296)		(12)	(±0.0037)		(14)	(±0.0255)		(13)	(±0.0027)		(7)	(±0.0259)		(12=)	(±0.0027)	
TempVel	-2117.3	-0.0034	NS	-35074	-0.0169	**	3399.7	+0.1002	*	-37510	+0.0094	NS	420.48	+0.0146	NS	-43828	-0.0066	NS	701.58	+0.0517	NS	-43903	-0.0097	*
	(11=)	(±0.0315)		(4=)	(±0.0059)		(4)	(±0.0417)		(4)	(±0.0052)		(10)	(±0.0358)		(8)	(±0.0038)		(5)	(±0.0363)		(5)	(±0.0038)	
PrecVel	-2117.3	-0.0045	NS	-35070	-0.0177	*	3405.0	+0.0413	NS	-37508	0.0066	NS	419.40	-0.0594	NS	-43827	-0.0087	NS	703.59	+0.0015	NS	-43900	-0.0117	*
	(11=)	(±0.0467)		(6)	(±0.0088)		(12=)	(±0.0618)		(7=)	(±0.0077)		(8)	(±0.0532)		(9)	(±0.0056)		(12=)	(±0.0539)		(6)	(±0.0056)	
HumArr	-2113.3	+0.0159	NS	-34982	+0.0189	*	3397.2	+0.0722	NS	-37471	-0.0492	****	410.69	-0.2088	****	-43717	-0.0122	*	688.65	-0.0794	NS	-43826	+0.0045	NS
	(14)	(±0.0410)		(15)	(±0.0075)		(3)	(±0.0535)		(13)	(±0.0066)		(6)	(±0.0464)		(15)	(±0.0048)		(2)	(±0.0476)		(15)	(±0.0049)	
CropHist	-2117.7	-0.0050	NS	-35066	+0.0074	*	3396.7	+0.0695	**	-37511	+0.0086	**	421.62	+0.0096	NS	-43832	+0.0078	***	703.08	-0.0016	NS	-43893	+0.0005	NS
	(9)	(±0.0177)		(8=)	(±0.0033)		(2)	(±0.0235)		(3)	(±0.0030)		(15)	(0.0202)		(6=)	(±0.0021)		(8)	(±0.0204)		(12=)	(±0.0021)	
GrassHist	-2120.0	+0.0352	NS	-35061	+0.0014	NS	3404.3	-0.0316	NS	-37504	-0.0051	NS	420.65	-0.0283	NS	-43819	+0.0007	NS	700.02	-0.0460	NS	-43893	-0.0008	NS
	(4)	(±0.0227)		(13=)	(±0.0042)		(11)	(±0.0300)		(11)	(±0.0037)		(13)	(±0.0258)		(14)	(±0.0027)		(4)	(±0.0262)		(12=)	(±0.0027)	

When testing each of the predictors in univariate models, the best-fitting predictor for the mean score of PCoA dimension one for all species was mean precipitation; areas of high precipitation were associated with lower mean scores of dimension one (Supplementary Table 5). The best fit predictor for resident species was mean NDVI; areas of high NDVI were associated with lower mean scores of dimension one. In the univariate models, very few of the contemporary variables had significant effects on the range of values for PCoA dimension one (Supplementary Table 6). The best-fit predictor for the range of PCoA dimension one in all species was mean precipitation; areas of high precipitation were associated with a greater range of PCoA dimension one scores. For resident species, the best fit predictor was NDVI seasonality; areas of high NDVI seasonality were associated with a greater range of PCoA dimension one scores.

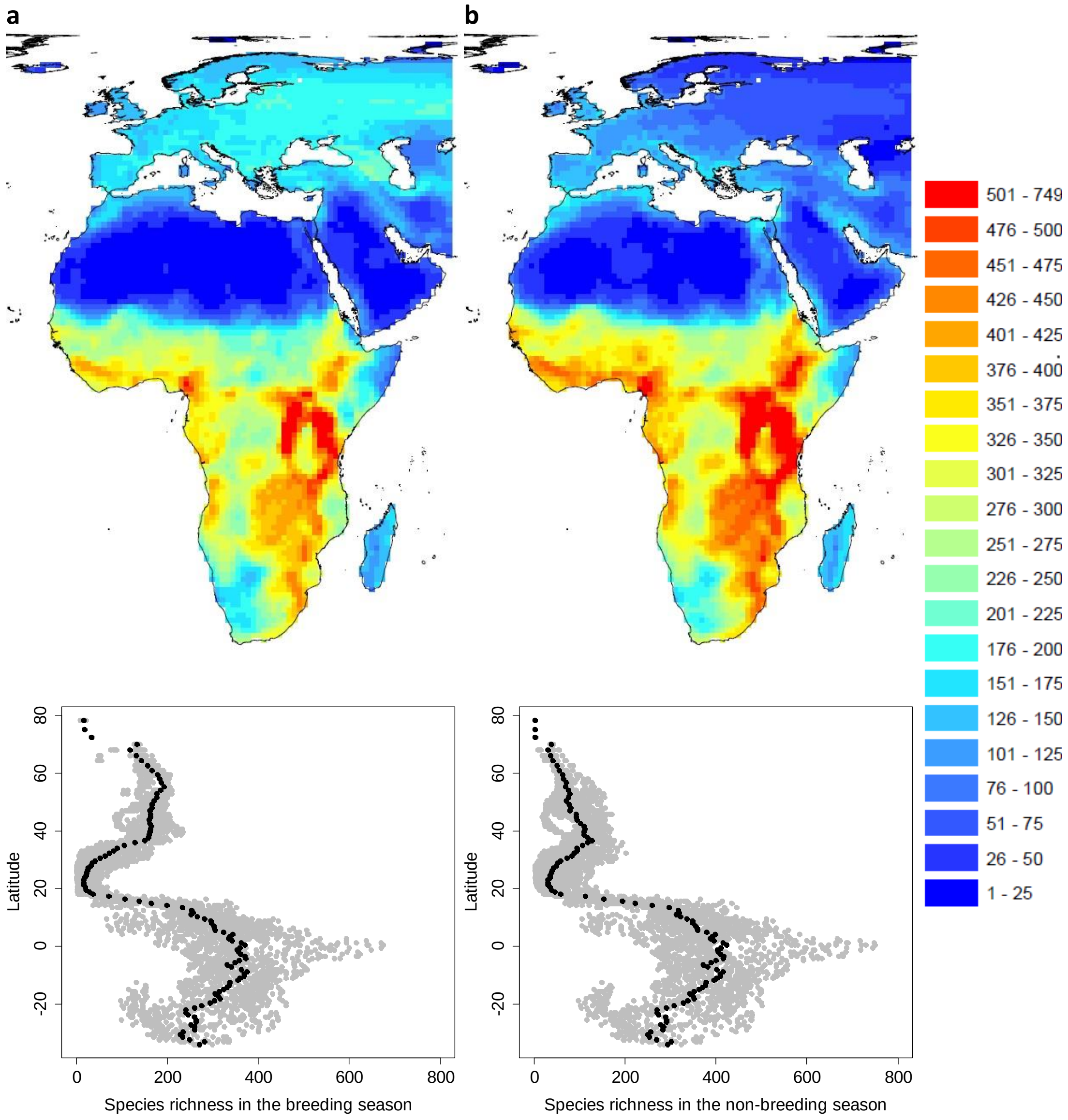
The univariate models for mean values of dimension two with the best fit predictors for all species and resident species were both seasonality; areas of high temperature seasonality were associated with low mean values of dimension two for all species and areas of high NDVI seasonality were associated with low mean values of dimension two for resident species (Supplementary Table 5). In the univariate models, some contemporary variables had contrasting effects on the range of PCoA dimension two for all species and resident species (Supplementary Table 6). The predictor with the best fit model for all species and resident species was temperature seasonality, but the effects were opposite; it had a significant positive association with the mean dimension two score for all species and a significant negative association for resident species.

Fewer of the univariate models showed significant effects on the mean score of PCoA dimension three for all species than for residents only (Supplementary Table 5). The best-fit predictor for all species was mean temperature, which showed a significant positive association. The best-fit predictor for resident species was mean NDVI, which had a significant negative association. Thus mean contemporary climate variables and their seasonality have a strong association with traits related to trophic level. In the univariate models, very few of the contemporary variables had significant effects on the range of values for PCoA dimension three for all species (Supplementary Table 6). For all species and resident species, the best-fit predictor was mean NDVI, but it had a significant negative association with the range of this dimension for all species and a significant positive association for resident species.

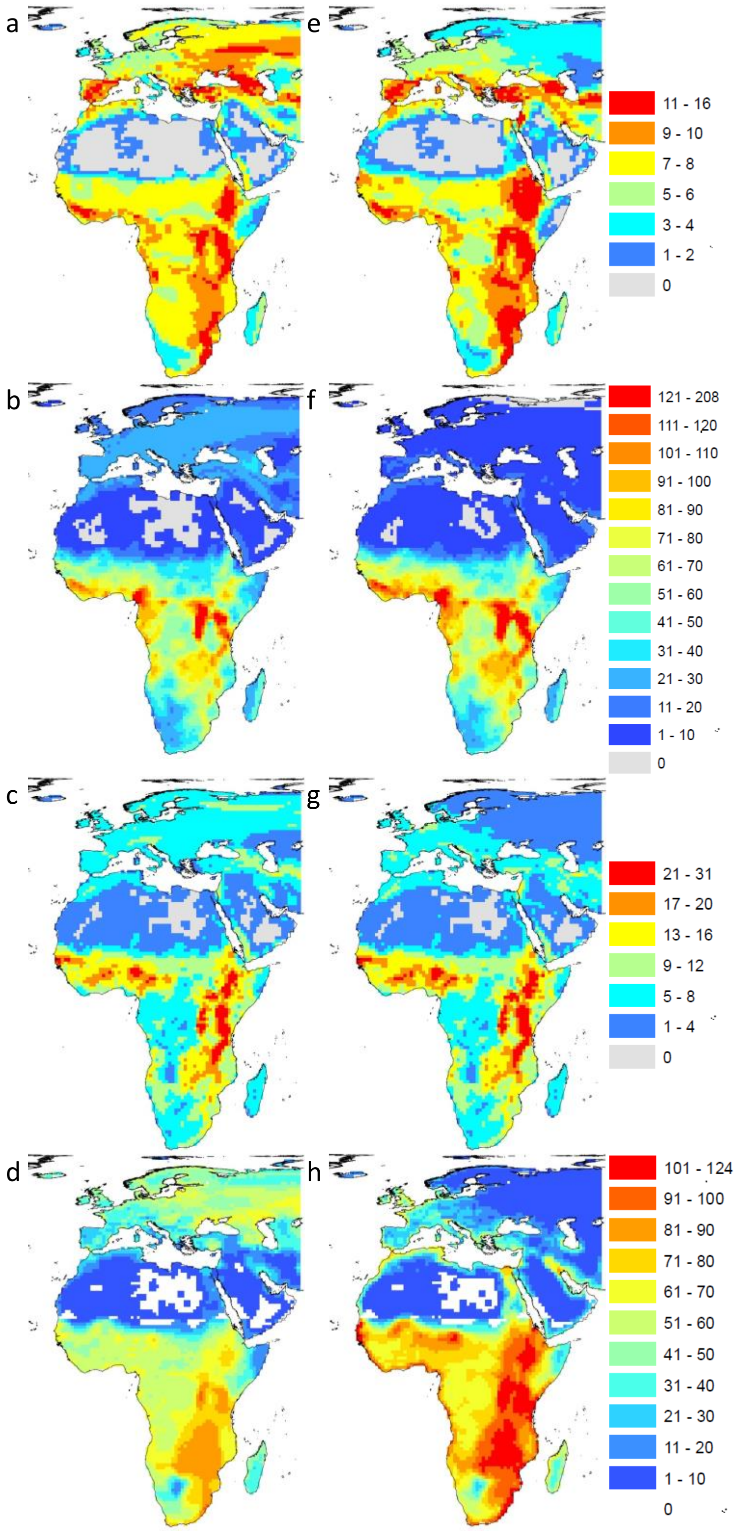
Almost all of the univariate models showed significant effects on the mean of PCoA dimension four, both for all species and residents only (Supplementary Table 5). Of these, the best-fitted predictor for all species was temperature change velocity. For resident species, the best-fitted predictor was temperature seasonality. There were very few univariate models with significant effects on the range of PCoA dimension four, particularly when all species were included (Supplementary Table 6). For all species, the best-fitted predictor was temperature seasonality. For resident species, the best-fitted predictor was NDVI seasonality.

Appendix S6: The seasonal changes in species richness and functional richness

The species richness in each season is shown in Supplementary Figure 5. Some cells show considerable community change. The greatest species richness changes are a loss of 156 species in the non-breeding season and a gain of 102 species in the non-breeding season.



Supplementary Figure 5: The species richness in the (a) breeding season and (b) non-breeding season.



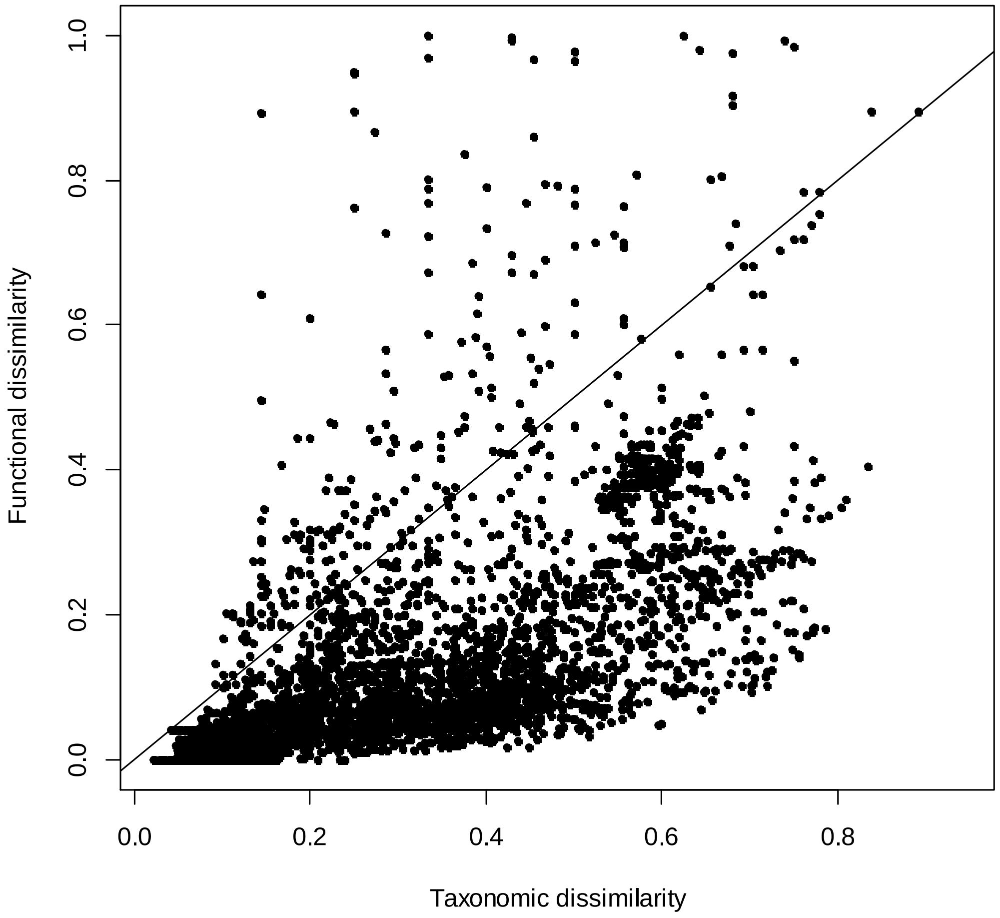
Supplementary Figure 6: Species richness in the (a-d) breeding season and (e-h) non-breeding season for (a&e) terrestrial predators, (b&f) terrestrial insectivores, (c&g) terrestrial herbivores and (d&h) aquatic foragers.

We also considered some less specialist groupings. Some birds that primarily forage on water may also forage on other substrates such as in low vegetation. Therefore wetlands may be important to them, but they are not so strictly tied to wet habitats. Additionally, many species that are primarily insectivorous also sometimes consume some fruit or berries when they are available. To test the appropriateness of our functional groups, we measured the functional metrics for non-exclusive aquatic foragers (303 species, 65.7% full migrants) and compared them with birds that only forage in/on water and we measured the functional metrics for insectivores that may also consume fruit and/or berries (815 species, 18.9% full migrants) and compared them to strictly insectivorous species.

The metrics were all significantly correlated at $p<0.0001$ (Supplementary Table 7). Most correlations were stronger than 0.6, except for SES_{FRic} for exclusive versus non-exclusive aquatic foragers, which showed weaker correlations. Based on these correlations, it was decided that the stricter groupings were appropriate for comparison.

Supplementary Table 7: Spearman's Rank Correlation Coefficients between the functional diversity metrics of (a) birds that forage in/on water exclusively and those that forage in/on water and may forage on other substrates and (b) birds that only eat insectivores and birds that eat insectivores and may also eat fruit and berries. All correlations were significant at $p < 0.0001$.

Metric	Correlation (R_s) between exclusive aquatic forager and non-exclusive aquatic foragers	Correlation (R_s) between exclusive insectivores and insectivores that may also eat fruit & berries
FRic breeding season	0.742	0.983
FRic non-breeding season	0.833	0.966
FEve breeding season	0.749	0.874
FEve non-breeding season	0.629	0.931
SES_{FRic} breeding season	0.290	0.727
SES_{FRic} non-breeding season	0.083	0.799
SES_{FEve} breeding season	0.790	0.891
SES_{FEve} non-breeding season	0.667	0.901



Supplementary Figure 7: The relationship between taxonomic dissimilarity and functional dissimilarity of cells in the breeding and non-breeding seasons. The line shows a theoretical 1:1 relationship.

Appendix S7: 95% confidence model sets for predicting local and large-scale responses to habitat disturbance

Supplementary Table 8: 95% confidence set of models predicting local extirpation (46 out of a total of 4096 possible combinations). AR = Altitudinal range, DB = Diet breadth, DH = Development at hatching, DT = Diet type, FD = Forest dependency, FL = Foraging location, GL = Generation length, HB = Habitat breadth, MS = Manmade site use, MV = Movement, WT = Weight, DS = Disturbance. * indicates that the variable appears in the model.

Model	Variables												ΔAIC	Akaike Weight (ω_i)	Cumulative $\Sigma\omega_i$
	AR	DB	DH	DT	FD	FL	GL	HB	MS	MV	WT	DS			
1		*	*		*			*	*	*	*	*	0.00	0.102	0.102
2		*	*		*		*	*	*	*	*	*	0.32	0.087	0.189
3	*	*	*		*			*	*	*	*	*	0.38	0.084	0.273
4	*	*	*		*		*	*	*	*	*	*	0.78	0.069	0.342
5		*	*		*		*	*	*	*		*	1.22	0.055	0.398
6		*	*		*	*	*	*	*	*		*	1.32	0.053	0.450
7		*	*		*	*	*	*	*	*	*	*	1.40	0.051	0.501
8	*	*	*		*	*	*	*	*	*	*	*	1.42	0.050	0.551
9	*	*	*		*	*	*	*	*	*		*	1.43	0.050	0.601
10	*	*	*		*	*		*	*	*	*	*	1.57	0.047	0.647
11		*	*		*	*		*	*	*	*	*	1.60	0.046	0.693
12	*	*	*		*		*	*	*	*		*	1.78	0.042	0.735
13	*	*	*	*	*			*	*	*	*	*	3.96	0.014	0.749
14		*	*	*	*			*	*	*	*	*	4.15	0.013	0.762
15	*	*	*	*	*		*	*	*	*	*	*	4.42	0.011	0.773
16	*	*	*	*	*		*	*	*	*		*	4.46	0.011	0.784
17		*	*	*	*		*	*	*	*		*	4.55	0.010	0.795
18		*	*	*	*		*	*	*	*	*	*	4.56	0.010	0.805
19		*	*		*			*	*	*		*	4.57	0.010	0.815
20		*	*		*	*		*	*	*		*	5.00	0.008	0.824
21	*	*	*	*	*	*	*	*	*	*		*	5.02	0.008	0.832
22	*	*	*		*			*	*	*		*	5.02	0.008	0.840

23	*	*	*		*	*		*	*	*		*	5.07	0.008	0.849
24			*		*		*	*	*	*		*	5.13	0.008	0.856
25			*		*	*	*	*	*	*		*	5.32	0.007	0.864
26		*	*	*	*	*	*	*	*	*		*	5.52	0.006	0.870
27			*		*			*	*	*	*	*	5.69	0.006	0.876
28	*	*	*	*	*	*	*	*	*	*	*	*	5.76	0.006	0.882
29	*	*	*	*	*	*		*	*	*	*	*	5.89	0.005	0.887
30			*		*		*	*	*	*	*	*	6.15	0.005	0.892
31			*	*	*		*	*	*	*		*	6.23	0.005	0.896
32		*	*	*	*	*	*	*	*	*	*	*	6.31	0.004	0.901
33	*		*		*	*	*	*	*	*		*	6.33	0.004	0.905
34		*	*	*	*	*		*	*	*	*	*	6.46	0.004	0.909
35	*		*		*		*	*	*	*		*	6.47	0.004	0.913
36	*		*	*	*		*	*	*	*		*	6.63	0.004	0.917
37			*	*	*			*	*	*	*	*	6.64	0.004	0.920
38			*		*	*		*	*	*	*	*	6.74	0.004	0.924
39			*		*	*	*	*	*	*	*	*	6.74	0.003	0.927
40			*		*			*	*	*		*	6.92	0.003	0.931
41	*	*	*	*	*			*	*	*		*	6.99	0.003	0.934
42	*		*		*			*	*	*	*	*	7.00	0.003	0.937
43	*		*	*	*			*	*	*	*	*	7.01	0.003	0.940
44		*	*	*	*			*	*	*		*	7.15	0.003	0.943
45			*	*	*		*	*	*	*	*	*	7.20	0.003	0.945
46			*	*	*	*	*	*	*	*		*	7.30	0.003	0.948

Supplementary Table 9: 95% confidence set of models predicting global threat status (168 out of a total of 32768 possible combinations). AR = Altitudinal range, DB = Diet breadth, DH = Development at hatching, DT = Diet type, FD = Forest dependency, FL = Foraging location, GL = Generation length, HB = Habitat breadth, MS = Manmade site use, MV = Movement, WT = Weight, AG = Proportion of agricultural landuse, UR = Proportion of urban landuse, PD = Human population density, HD = Proportion of range with high human population density. * indicates that the variable appears in the model.

Model	**Variables**															**ΔAIC**	**Akaike Weight**	**Cumulative**
	AR	DB	DH	DT	FD	FL	GL	HB	MS	MV	WT	AG	UR	PD	HD		**(ω_i)**	**$\Sigma\omega_i$**
1	*	*	*	*	*	*		*			*	*	*		*	0.00	0.056	0.056
2	*	*	*	*	*	*		*		*	*	*	*		*	0.67	0.040	0.096
3	*	*	*	*	*	*		*			*	*	*	*	*	0.86	0.037	0.133
4	*	*		*	*	*		*			*	*	*		*	1.35	0.029	0.161
5	*	*	*	*	*	*	*	*			*	*	*		*	1.44	0.027	0.189
6	*	*	*	*	*			*			*	*	*		*	1.62	0.025	0.214
7	*	*		*	*	*		*		*	*	*	*		*	1.79	0.023	0.237
8	*	*	*	*	*	*		*	*		*	*	*		*	1.91	0.022	0.258
9	*	*	*	*	*			*		*	*	*	*		*	1.96	0.021	0.279
10	*	*	*	*	*	*		*		*	*	*	*	*	*	1.96	0.021	0.301
11	*	*	*	*	*	*	*	*		*	*	*	*		*	2.12	0.019	0.320
12	*	*		*	*	*		*			*	*	*	*	*	2.15	0.019	0.339
13	*	*	*	*	*	*	*	*			*	*	*	*	*	2.29	0.018	0.357
14	*	*	*	*	*	*		*	*	*	*	*	*		*	2.56	0.016	0.373
15	*	*	*	*	*			*			*	*	*	*	*	2.58	0.015	0.388
16	*	*		*	*	*	*	*			*	*	*		*	2.72	0.014	0.402
17	*	*	*	*	*	*		*	*		*	*	*	*	*	2.80	0.014	0.416
18	*	*	*	*	*		*	*			*	*	*		*	3.00	0.013	0.429
19	*	*		*	*	*		*		*	*	*	*	*	*	3.06	0.012	0.441
20	*	*		*	*			*			*	*	*		*	3.12	0.012	0.453
21	*	*		*	*	*		*	*		*	*	*		*	3.15	0.012	0.464
22	*	*		*	*			*		*	*	*	*		*	3.15	0.012	0.476
23	*	*		*	*	*	*	*		*	*	*	*		*	3.19	0.011	0.488

24	*	*	*	*	*			*		*	*	*	*	*	*	3.33	0.011	0.498
25	*	*	*	*	*	*	*	*	*		*	*	*		*	3.35	0.011	0.509
26	*	*	*	*	*		*	*		*	*	*	*		*	3.35	0.011	0.519
27	*	*	*	*	*	*	*	*		*	*	*	*	*	*	3.40	0.010	0.529
28	*	*		*	*	*	*	*			*	*	*	*	*	3.51	0.010	0.539
29	*	*		*	*	*		*	*	*	*	*	*		*	3.55	0.010	0.549
30	*		*	*	*			*			*	*	*		*	3.60	0.009	0.558
31	*	*	*	*	*			*	*		*	*	*		*	3.61	0.009	0.567
32	*		*	*	*	*		*			*	*	*		*	3.73	0.009	0.576
33	*	*	*	*	*	*		*	*	*	*	*	*	*	*	3.88	0.008	0.584
34	*		*	*	*			*		*	*	*	*		*	3.92	0.008	0.592
35	*	*	*	*	*			*	*	*	*	*	*		*	3.94	0.008	0.600
36	*	*	*	*	*		*	*			*	*	*	*	*	3.95	0.008	0.607
37	*	*		*	*	*		*	*		*	*	*	*	*	3.99	0.008	0.615
38	*	*	*	*	*	*	*	*	*	*	*	*	*		*	4.01	0.008	0.623
39	*	*		*	*			*			*	*	*	*	*	4.03	0.007	0.630
40	*	*	*	*	*	*	*	*	*		*	*	*	*	*	4.23	0.007	0.637
41	*		*	*	*	*		*		*	*	*	*		*	4.37	0.006	0.643
42	*	*		*	*		*	*			*	*	*		*	4.43	0.006	0.649
43	*	*		*	*	*	*	*		*	*	*	*	*	*	4.44	0.006	0.655
44	*	*		*	*		*	*		*	*	*	*		*	4.50	0.006	0.661
45	*			*	*	*		*			*	*	*		*	4.51	0.006	0.667
46	*	*		*	*			*		*	*	*	*	*	*	4.52	0.006	0.673
47	*	*		*	*	*	*	*	*		*	*	*		*	4.52	0.006	0.679
48	*	*	*	*	*			*	*		*	*	*	*	*	4.58	0.006	0.685
49	*	*	*	*	*	*		*			*		*		*	4.61	0.006	0.690
50	*			*	*			*			*	*	*		*	4.61	0.006	0.696
51	*		*	*	*			*			*	*	*	*	*	4.68	0.005	0.701
52	*			*	*			*		*	*	*	*		*	4.69	0.005	0.707
53	*	*	*	*	*		*	*		*	*	*	*	*	*	4.71	0.005	0.712
54	*		*	*	*	*		*			*	*	*	*	*	4.74	0.005	0.717
55	*		*	*	*		*	*			*	*	*		*	4.84	0.005	0.722

56	*	*		*	*	*		*	*	*	*	*	*	*	*	4.86	0.005	0.727
57	*	*		*	*	*	*	*	*	*	*	*	*		*	4.95	0.005	0.732
58	*			*	*	*		*		*	*	*	*		*	4.98	0.005	0.737
59	*		*	*	*	*	*	*			*	*	*		*	4.99	0.005	0.741
60	*	*	*	*	*		*	*	*		*	*	*		*	4.99	0.005	0.746
61	*	*		*	*			*	*		*	*	*		*	5.05	0.004	0.750
62	*	*		*	*			*	*	*	*	*	*		*	5.07	0.004	0.755
63	*		*	*	*		*	*		*	*	*	*		*	5.19	0.004	0.759
64	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	5.31	0.004	0.763
65	*	*	*	*	*			*	*	*	*	*	*	*	*	5.32	0.004	0.767
66	*	*	*	*	*		*	*	*	*	*	*	*		*	5.34	0.004	0.771
67	*	*		*	*		*	*			*	*	*	*	*	5.34	0.004	0.775
68	*	*		*	*	*	*	*	*		*	*	*	*	*	5.36	0.004	0.778
69	*		*	*	*			*		*	*	*	*	*	*	5.39	0.004	0.782
70	*			*	*	*		*			*	*	*	*	*	5.46	0.004	0.786
71	*		*	*	*			*	*		*	*	*		*	5.59	0.003	0.789
72	*		*	*	*	*		*	*		*	*	*		*	5.64	0.003	0.793
73	*			*	*			*			*	*	*	*	*	5.65	0.003	0.796
74	*		*	*	*	*	*	*		*	*	*	*		*	5.66	0.003	0.799
75	*	*		*	*	*		*			*		*		*	5.66	0.003	0.803
76	*			*	*	*	*	*			*	*	*		*	5.72	0.003	0.806
77	*		*	*	*	*		*		*	*	*	*	*	*	5.77	0.003	0.809
78	*			*	*		*	*			*	*	*		*	5.81	0.003	0.812
79	*	*		*	*		*	*		*	*	*	*	*	*	5.85	0.003	0.815
80	*		*	*	*			*	*	*	*	*	*		*	5.91	0.003	0.818
81	*		*	*	*		*	*			*	*	*	*	*	5.91	0.003	0.821
82	*			*	*		*	*		*	*	*	*		*	5.92	0.003	0.824
83	*	*	*	*	*		*	*	*		*	*	*	*	*	5.95	0.003	0.827
84	*		*	*	*	*	*	*			*	*	*	*	*	5.99	0.003	0.830
85	*	*		*	*			*	*		*	*	*	*	*	5.99	0.003	0.832
86	*	*	*	*	*	*	*	*			*		*		*	6.07	0.003	0.835
87	*	*	*	*	*	*		*			*	*		*	*	6.13	0.003	0.838

88	*			*	*			*		*	*	*	*	*	*	6.14	0.003	0.840
89	*			*	*	*	*	*		*	*	*	*		*	6.22	0.003	0.843
90	*	*		*	*	*	*	*	*	*	*	*	*	*	*	6.25	0.002	0.845
91	*		*	*	*	*		*	*	*	*	*	*		*	6.26	0.002	0.848
92	*			*	*	*		*	*		*	*	*		*	6.31	0.002	0.850
93	*			*	*	*		*		*	*	*	*	*	*	6.36	0.002	0.852
94	*	*		*	*		*	*	*		*	*	*		*	6.37	0.002	0.855
95	*	*	*		*	*		*			*	*	*		*	6.39	0.002	0.857
96	*	*		*	*		*	*	*	*	*	*	*		*	6.41	0.002	0.859
97	*	*	*	*	*	*		*		*	*		*		*	6.43	0.002	0.862
98	*	*		*	*			*	*	*	*	*	*	*	*	6.46	0.002	0.864
99	*	*	*	*	*	*		*			*		*	*	*	6.47	0.002	0.866
100	*			*	*			*	*		*	*	*		*	6.54	0.002	0.868
101	*	*	*	*	*	*		*	*		*		*		*	6.57	0.002	0.870
102	*			*	*			*	*	*	*	*	*		*	6.60	0.002	0.872
103	*		*	*	*		*	*		*	*	*	*	*	*	6.64	0.002	0.874
104	*			*	*	*	*	*			*	*	*	*	*	6.66	0.002	0.876
105	*		*	*	*	*		*	*		*	*	*	*	*	6.67	0.002	0.878
106	*		*	*	*			*	*		*	*	*	*	*	6.68	0.002	0.880
107	*	*	*	*	*		*	*	*	*	*	*	*	*	*	6.71	0.002	0.882
108	*			*	*	*		*	*	*	*	*	*		*	6.76	0.002	0.884
109	*		*	*	*		*	*	*		*	*	*		*	6.83	0.002	0.886
110	*			*	*		*	*			*	*	*	*	*	6.83	0.002	0.888
111	*		*	*	*	*	*	*	*		*	*	*		*	6.90	0.002	0.890
112	*	*	*		*	*		*			*	*	*	*	*	6.93	0.002	0.891
113	*		*	*	*	*	*	*		*	*	*	*	*	*	7.05	0.002	0.893
114	*	*		*	*	*	*	*			*		*		*	7.06	0.002	0.895
115	*	*		*	*	*		*		*	*		*		*	7.17	0.002	0.896
116	*		*	*	*		*	*	*	*	*	*	*		*	7.18	0.002	0.898
117	*	*		*	*	*		*			*	*		*	*	7.29	0.001	0.899
118	*			*	*	*		*	*		*	*	*	*	*	7.30	0.001	0.901
119	*	*		*	*		*	*	*		*	*	*	*	*	7.30	0.001	0.902

120	*			*	*		*	*		*	*	*	*	*	*	7.36	0.001	0.904
121	*		*	*	*			*	*	*	*	*	*	*	*	7.38	0.001	0.905
122	*	*	*	*	*			*			*		*		*	7.44	0.001	0.906
123	*	*		*	*	*		*			*		*	*	*	7.49	0.001	0.908
124	*	*	*		*	*		*		*	*	*	*		*	7.52	0.001	0.909
125	*			*	*	*	*	*	*		*	*	*		*	7.53	0.001	0.910
126	*		*	*	*	*	*	*	*	*	*	*	*		*	7.55	0.001	0.912
127	*	*		*	*	*		*	*		*		*		*	7.55	0.001	0.913
128	*			*	*	*	*	*		*	*	*	*	*	*	7.59	0.001	0.914
129	*			*	*			*	*		*	*	*	*	*	7.60	0.001	0.915
130	*	*	*	*	*	*	*	*			*	*		*	*	7.67	0.001	0.917
131	*		*	*	*	*		*	*	*	*	*	*	*	*	7.69	0.001	0.918
132	*			*	*		*	*	*		*	*	*		*	7.74	0.001	0.919
133	*	*		*	*		*	*	*	*	*	*	*	*	*	7.79	0.001	0.920
134	*			*	*		*	*	*	*	*	*	*		*	7.84	0.001	0.921
135	*		*	*	*	*		*			*		*		*	7.87	0.001	0.922
136	*		*	*	*		*	*	*		*	*	*	*	*	7.91	0.001	0.923
137	*	*	*	*	*	*	*	*			*		*	*	*	7.93	0.001	0.925
138	*		*	*	*	*	*	*	*		*	*	*	*	*	7.93	0.001	0.926
139	*	*	*	*	*	*	*	*		*	*		*		*	7.94	0.001	0.927
140	*			*	*	*	*	*	*	*	*	*	*		*	8.00	0.001	0.928
141	*	*	*	*	*	*	*	*	*		*		*		*	8.03	0.001	0.929
142	*	*	*	*	*	*		*	*		*	*		*	*	8.03	0.001	0.930
143	*	*	*		*	*	*	*			*	*	*		*	8.06	0.001	0.931
144	*			*	*			*	*	*	*	*	*	*	*	8.08	0.001	0.932
145	*			*	*	*		*	*	*	*	*	*	*	*	8.17	0.001	0.933
146	*	*	*		*	*		*	*		*	*	*		*	8.19	0.001	0.934
147	*	*	*	*	*			*			*	*		*	*	8.36	0.001	0.934
148	*	*	*	*	*	*		*	*	*	*		*		*	8.39	0.001	0.935
149	*			*	*	*		*			*		*		*	8.42	0.001	0.936
150	*	*	*	*	*	*		*		*	*		*	*	*	8.42	0.001	0.937
151	*	*	*	*	*	*		*	*		*		*	*	*	8.44	0.001	0.938

152	*			*	*	*	*	*	*		*	*	*	*	*	8.51	0.001	0.939
153	*	*	*		*	*		*		*	*	*	*	*	*	8.53	0.001	0.939
154	*	*	*		*	*	*	*			*	*	*	*	*	8.59	0.001	0.940
155	*		*	*	*		*	*	*	*	*	*	*	*	*	8.64	0.001	0.941
156	*	*		*	*	*	*	*		*	*		*		*	8.64	0.001	0.942
157	*	*		*	*			*			*		*		*	8.70	0.001	0.942
158	*	*			*	*		*			*	*	*		*	8.70	0.001	0.943
159	*	*		*	*	*	*	*			*	*		*	*	8.77	0.001	0.944
160	*	*	*		*	*		*	*		*	*	*	*	*	8.78	0.001	0.944
161	*			*	*		*	*	*		*	*	*	*	*	8.79	0.001	0.945
162	*	*	*	*	*		*	*			*		*		*	8.85	0.001	0.946
163	*	*	*	*	*			*		*	*		*		*	8.86	0.001	0.947
164	*	*		*	*	*	*	*			*		*	*	*	8.89	0.001	0.947
165	*		*	*	*			*			*		*		*	8.94	0.001	0.948
166	*	*		*	*	*	*	*	*		*		*		*	8.95	0.001	0.948
167	*		*	*	*	*	*	*	*	*	*	*	*	*	*	8.96	0.001	0.949
168	*	*		*	*	*		*	*	*	*		*		*	9.06	0.001	0.950

Appendix S8: List of species that are predicted to be locally sensitive, but globally are of Least Concern.

Supplementary Table 10: List of species that are predicted to be locally sensitive, but globally are of Least Concern. These species are in the lowest quartile of predicted sensitivity for LC species using the local scale model and as such there is no cut-off for sensitive versus resistant; species are predicted as being on a continuum and these species are the most sensitive of the LC group.

Order	Family	Species
Anseriformes	Anatidae	*Aix galericulata*
		Anas gibberifrons
		Anas gracilis
		Anas poecilorhyncha
		Anas zonorhyncha
		Anser indicus
		Dendrocygna arcuata
		Dendrocygna bicolor
		Dendrocygna guttata
		Dendrocygna javanica
		Nettapus coromandelianus
		Tadorna ferruginea
		Tadorna radjah
Apodiformes	Hemiprocnidae	*Hemiprocne mystacea*
Apodimorphae	Apodidae	*Apus nipalensis*
		Apus pacificus
		Hirundapus caudacutus
		Hirundapus cochinchinensis
Bucerotiformes	Bucerotidae	*Aceros plicatus*
		Aceros undulatus
		Anorrhinus galeritus
		Penelopides affinis
		Penelopides exarhatus
		Penelopides manillae
		Penelopides samarensis
Charadriiformes	Alcidae	*Synthliboramphus antiquus*
	Ibidorhynchidae	*Ibidorhyncha struthersii*
	Recurvirostridae	*Himantopus himantopus*
		Himantopus leucocephalus
		Recurvirostra avosetta
Ciconiiformes	Accipitridae	*Accipiter erythrauchen*
		Accipiter fasciatus
		Accipiter gentilis
		Accipiter griseiceps
		Accipiter meyerianus
		Accipiter nisus
		Accipiter novaehollandiae
		Accipiter rhodogaster
		Accipiter soloensis
		Accipiter trinotatus
		Accipiter trivirgatus
		Accipiter virgatus
		Aquila chrysaetos
		Aquila fasciatus
		Aquila rapax
		Aviceda jerdoni
		Aviceda leuphotes
		Buteo buteo
		Buteo hemilasius
		Buteo rufinus
		Circaetus gallicus
		Circus assimilis
		Gypaetus barbatus

		Gyps fulvus
		Gyps himalayensis
		Hieraaetus pennatus
		Ictinaetus malayensis
		Lophotriorchis kienerii
		Macheiramphus alcinus
		Nisaetus alboniger
		Nisaetus cirrhatus
		Nisaetus lanceolatus
		Nisaetus nipalensis
		Pandion haliaetus
		Pernis celebensis
		Pernis ptilorhyncus
		Spilornis cheela
		Spilornis holospilus
		Spilornis rufipectus
	Anhingidae	*Anhinga novaehollandiae*
	Ardeidae	*Ardea purpurea*
		Ardea sumatrana
		Ardeola bacchus
		Ardeola speciosa
		Butorides striata
		Egretta gularis
		Gorsachius melanolophus
		Ixobrychus cinnamomeus
		Ixobrychus eurhythmus
		Ixobrychus flavicollis
	Burhinidae	*Burhinus oedicnemus*
		Esacus recurvirostris
	Charadriidae	*Charadrius mongolus*
		Vanellus cinereus
		Vanellus indicus
		Vanellus malarbaricus
	Ciconiidae	*Anastomus oscitans*
		Ciconia episcopus
	Falconidae	*Falco longipennis*
		Falco pelegrinoides
		Falco severus
		Falco subbuteo
		Microhierax caerulescens
		Microhierax erythrogenys
		Microhierax fringillarius
		Microhierax melanoleucos
	Glareolidae	*Glareola lactea*
		Glareola maldivarum
	Jacanidae	*Hydrophasianus chirurgus*
		Irediparra gallinacea
		Metopidius indicus
	Laridae	*Chlidonias hybrida*
		Larus brunnicephalus
		Larus crassirostris
		Sterna albifrons
		Sterna anaethetus
		Sterna aurantia
		Sterna bengalensis
		Sterna bergii
		Sterna caspia
		Sterna dougallii
		Sterna hirundo
		Sterna saundersi
		Sterna sumatrana
	Pelecanidae	*Pelecanus onocrotalus*
	Phalacrocoracidae	*Phalacrocorax carbo*
		Phalacrocorax fuscicollis
		Phalacrocorax niger
		Phalacrocorax sulcirostris
	Phoenicopteridae	*Phoenicopterus roseus*
	Podicipedidae	*Podiceps cristatus*
		Tachybaptus novaehollandiae
	Rostratulidae	*Rostratula benghalensis*
	Scolopacidae	*Scolopax bukidnonensis*

		Scolopax rusticola
		Tringa totanus
	Threskiornithidae	*Platalea leucorodia*
Columbiformes	Columbidae	*Chalcophaps stephani*
		Cryptophaps poecilorrhoa
		Ducula badia
		Ducula bicolor
		Ducula forsteni
		Ducula lacernulata
		Ducula luctuosa
		Ducula perspicillata
		Ducula radiata
		Gallicolumba tristigmata
		Gymnophaps mada
		Macropygia magna
		Macropygia tenuirostris
		Phapitreron amethystinus
		Phapitreron leucotis
		Ptilinopus cinctus
		Ptilinopus fischeri
		Ptilinopus leclancheri
		Ptilinopus occipitalis
		Ptilinopus porphyreus
		Ptilinopus regina
		Ptilinopus rivoli
		Ptilinopus superbus
		Reinwardtoena reinwardtsi
		Treron apicauda
		Treron olax
		Treron pompadora
		Treron seimundi
		Treron sphenurus
		Turacoena manadensis
Coraciiformes	Alcedinidae	*Actenoides princeps*
		Alcedo cyanopectus
		Megaceryle lugubris
	Meropidae	*Meropogon forsteni*
Craciformes	Megapodiidae	*Megapodius cumingii*
Cuculiformes	Cuculidae	*Chrysococcyx maculatus*
		Cuculus canorus
		Cuculus crassirostris
		Cuculus fugax
		Cuculus lepidus
		Cuculus poliocephalus
		Phaenicophaeus cumingi
		Scythrops novaehollandiae
		Surniculus lugubris
Galliformes	Phasianidae	*Alectoris chukar*
		Ammoperdix griseogularis
		Arborophila brunneopectus
		Arborophila cambodiana
		Arborophila campbelli
		Arborophila chloropus
		Arborophila hyperythra
		Arborophila javanica
		Arborophila rolli
		Arborophila rubrirostris
		Arborophila rufogularis
		Arborophila sumatrana
		Arborophila torqueola
		Bambusicola fytchii
		Bambusicola thoracicus
		Chrysolophus amherstiae
		Chrysolophus pictus
		Coturnix chinensis
		Coturnix coromandelica
		Coturnix ypsilophora
		Francolinus pintadeanus
		Galloperdix bicalcarata
		Galloperdix lunulata
		Galloperdix spadicea

		Gallus gallus
		Gallus lafayetii
		Gallus sonneratii
		Gallus varius
		Haematortyx sanguiniceps
		Ithaginis cruentus
		Lerwa lerwa
		Lophophorus impejanus
		Lophura nycthemera
		Pavo cristatus
		Perdicula argoondah
		Perdicula asiatica
		Perdicula erythrorhyncha
		Phasianus colchicus
		Polyplectron bicalcaratum
		Polyplectron chalcurum
		Pucrasia macrolopha
		Tetraogallus himalayensis
		Tetraogallus tibetanus
		Tetraophasis szechenyii
		Tragopan temminckii
Gruiformes	Rallidae	*Amaurornis akool*
		Amaurornis bicolor
		Amaurornis moluccana
		Amaurornis olivacea
		Rallina eurizonoides
		Rallina fasciata
Passeriformes	Alaudidae	*Calandrella cheleensis*
	Campephagidae	*Coracina abbotti*
		Coracina dohertyi
	Certhiidae	*Certhia familiaris*
		Certhia hodgsoni
		Certhia nipalensis
		Salpornis spilonotus
	Cinclidae	*Cinclus cinclus*
		Cinclus pallasii
	Corvidae	*Cissa hypoleuca*
		Cissa thalassina
		Temnurus temnurus
		Urocissa caerulea
	Eurylaimidae	*Psarisomus dalhousiae*
		Serilophus lunatus
	Fringillidae	*Loxia curvirostra*
		Mycerobas melanozanthos
		Pyrrhula nipalensis
	Irenidae	*Irena cyanogastra*
	Meliphagidae	*Myza celebensis*
		Myzomela wakoloensis
		Philemon moluccensis
		Philemon subcorniculatus
	Muscicapidae	*Cinclidium diana*
		Cyornis unicolor
		Enicurus immaculatus
		Enicurus scouleri
		Enicurus velatus
		Luscinia brunnea
		Muscicapa ferruginea
		Muscicapa muttui
		Muscicapa ruficauda
		Niltava sundara
	Pachycephalidae	*Coracornis raveni*
		Pachycephala albiventris
		Pachycephala homeyeri
		Pachycephala sulfuriventer
	Paridae	*Parus rufonuchalis*
	Passeridae	*Passer rutilans*
	Pittidae	*Pitta arcuata*
		Pitta cyanea
		Pitta elegans
		Pitta erythrogaster
		Pitta oatesi

		Pitta phayrei
	Pycnonotidae	*Pycnonotus striatus*
	Rhipiduridae	*Rhipidura hypoxantha*
	Sturnidae	*Basilornis corythaix*
		Sarcops calvus
		Saroglossa spiloptera
	Sylviidae	*Bradypterus caudatus*
		Cettia major
		Hippolais rama
		Phylloscopus emeiensis
		Phylloscopus forresti
		Phylloscopus magnirostris
		Phylloscopus occipitalis
		Seicercus poliogenys
		Seicercus soror
		Seicercus valentini
		Urosphena whiteheadi
	Timaliidae	*Actinodura souliei*
		Cutia nipalensis
		Garrulax affinis
		Garrulax calvus
		Garrulax castanotis
		Garrulax delesserti
		Garrulax maesi
		Garrulax palliatus
		Gypsophila crispifrons
		Heterophasia annectens
		Heterophasia auricularis
		Heterophasia melanoleuca
		Heterophasia pulchella
		Leonardina woodi
		Malia grata
		Napothera epilepidota
		Pnoepyga immaculata
		Pnoepyga pusilla
		Pomatorhinus erythrocnemis
		Pomatorhinus ferruginosus
		Pteruthius flaviscapis
		Pteruthius melanotis
		Pteruthius rufiventer
		Pteruthius xanthochlorus
		Ptilocichla mindanensis
		Rimator albostriatus
		Rimator pasquieri
		Spelaeornis kinneari
		Stachyris ruficeps
		Turdinus marmorata
		Turdinus rufipectus
	Turdidae	*Cochoa purpurea*
		Cochoa viridis
		Heinrichia calligyna
		Myophonus borneensis
		Myophonus glaucinus
		Turdus rubrocanus
		Zoothera dixoni
		Zoothera marginata
		Zoothera monticola
	Zosteropidae	*Lophozosterops dohertyi*
		Lophozosterops goodfellowi
		Lophozosterops squamiceps
		Oculocincta squamifrons
Piciformes	Picidae	*Blythipicus pyrrhotis*
		Dendrocopos canicapillus
		Dendrocopos darjellensis
		Dendrocopos hyperythrus
		Dryocopus javensis
		Gecinulus grantia
		Hemicircus concretus
		Mulleripicus fulvus
		Mulleripicus funebris
		Picus viridanus

	Ramphastidae	*Megalaima corvina*
		Megalaima eximia
		Megalaima faiostricta
		Megalaima franklinii
		Megalaima incognita
		Megalaima lagrandieri
		Megalaima pulcherrima
Pteroclidiformes	Pteroclididae	*Pterocles exustus*
		Pterocles indicus
		Pterocles senegallus
Strigiformes	Caprimulgidae	*Caprimulgus affinis*
		Caprimulgus asiaticus
		Caprimulgus atripennis
		Caprimulgus celebensis
		Caprimulgus europaeus
		Caprimulgus indicus
		Caprimulgus manillensis
		Eurostopodus macrotis
		Eurostopodus temminckii
	Podargidae	*Batrachostomus affinis*
		Batrachostomus cornutus
		Batrachostomus hodgsoni
		Batrachostomus javensis
		Batrachostomus moniliger
		Batrachostomus septimus
	Strigidae	*Bubo bengalensis*
		Bubo bubo
		Bubo coromandus
		Bubo nipalensis
		Bubo sumatranus
		Glaucidium brodiei
		Glaucidium castanopterum
		Ketupa flavipes
		Ketupa ketupu
		Ketupa zeylonensis
		Ninox novaeseelandiae
		Ninox punctulata
		Ninox squamipila
		Otus brookii
		Otus magicus
		Otus manadensis
		Otus megalotis
		Otus spilocephalus
		Strix leptogrammica
		Strix ocellata
	Tytonidae	*Tyto rosenbergii*
Trogoniformes	Trogonidae	*Apalharpactes mackloti*
Turniciformes	Turnicidae	*Turnix maculosus*
		Turnix sylvaticus
		Turnix tanki

Appendix S9: List of gap species

Supplementary Table 11: A list of Gap species (those whose geographic range does not coincide with a protected area in IUCN categories I-IV). Species marked with an asterisk would be protected if all BirdLife International Important Bird and Biodiversity areas were given the same legal protection as IUCN categories I-IV. CR= Critically endangered, EN = Endangered, VU = Vulnerable to extinction, NT = Near threatened, LC = Least concern, DD = Data deficient.

Order	Family	Species	Threat status
Anseriformes	Anatidae	*Aythya innotata*	CR
		Rhodonessa caryophyllacea	CR
		Tadorna cristata	CR
Apodimorphae	Apodidae	*Apus berliozi**	LC
		Collocalia orientalis	DD
Ciconiiformes	Accipitridae	*Accipiter brachyurus*	VU
		Accipiter imitator	VU
		Accipiter luteoschistaceus	VU
		Accipiter princeps	VU
		Henicopernis infuscatus	VU
	Charadriidae	*Vanellus macropterus*	CR
	Laridae	*Larus atlanticus**	VU
		*Sterna bernsteini**	CR
		*Sterna lorata**	EN
	Podicipedidae	*Podiceps taczanowskii**	CR
	Scolopacidae	*Numenius borealis*	CR
	Sulidae	*Sula variegata**	LC
	Threskiornithidae	*Geronticus eremita**	CR
		Nipponia nippon	EN
Columbiformes	Columbidae	*Columba oliviae**	DD
		*Ducula cineracea**	EN
		Ducula finschii	NT
		Ducula melanochroa	LC
		Ducula subflavescens	NT
		Geotrygon carrikeri	EN
		Gymnophaps solomonensis	LC
		Henicophaps foersteri	VU
		*Leptotila conoveri**	EN
		*Patagioenas caribaea**	VU
		*Patagioenas oenops**	VU
		Ptilinopus insolitus	LC
		Reinwardtoena browni	NT
Coraciiformes	Alcedinidae	*Actenoides bougainvillei*	VU
		Alcedo websteri	VU
		Tanysiptera danae	LC
		Todiramphus albonotatus	NT
	Brachypteraciidae	*Uratelornis chimaera**	VU
Craciformes	Megapodiidae	*Megapodius bernsteinii**	NT
Cuculiformes	Cuculidae	*Centropus ateralbus*	LC
		Centropus violaceus	NT
Galliformes	Odontophoridae	*Odontophorus hyperythrus*	NT
	Phasianidae	*Alectoris magna**	LC
		*Arborophila ardens**	VU
		*Arborophila gingica**	VU
		*Arborophila rufipectus**	EN
		*Bonasa sewerzowi**	NT
		*Crossoptilon auritum**	LC
		*Crossoptilon mantchuricum**	VU
		*Francolinus griseostriatus**	NT
		*Francolinus ochropectus**	CR
		*Francolinus swierstrai**	EN
		*Lophophorus lhuysii**	VU
		*Polyplectron katsumatae**	EN

		*Syrmaticus ellioti**	NT
		*Syrmaticus reevesii**	VU
		*Tetraophasis obscurus**	LC
		*Tragopan caboti**	VU
Gruiformes	Mesitornithidae	*Monias benschi**	VU
	Otididae	*Eupodotis humilis**	NT
	Rallidae	*Cyanolimnas cerverai**	CR
		Gallirallus insignis	NT
		Gallirallus lafresnayanus	CR
		*Laterallus tuerosi**	EN
Passeriformes	Aegithalidae	*Aegithalos fuliginosus**	LC
	Alaudidae	*Alaemon hamertoni**	LC
		Heteromirafra archeri	CR
		*Heteromirafra sidamoensis**	CR
		*Mirafra ashi**	EN
		*Spizocorys obbiensis**	DD
	Artamidae	*Artamus insignis*	LC
	Campephagidae	*Coracina fortis**	NT
		*Coracina schistacea**	LC
	Cardinalidae	*Amaurospiza carrizalensis**	CR
	Certhiidae	*Certhia tianquanensis**	NT
	Cisticolidae	*Apalis flavigularis**	EN
		*Apalis fuscigularis**	CR
		*Apalis lynesi**	NT
		*Rhopophilus pekinensis**	LC
	Colluricinclidae	*Pitohui incertus*	NT
	Corvidae	*Corvus meeki*	LC
		Corvus unicolor	CR
		Cyanocorax dickeyi	NT
		Cyanolyca mirabilis	VU
		*Perisoreus internigrans**	VU
		*Podoces biddulphi**	NT
	Cotingidae	*Lipaugus weberi*	EN
	Dicaeidae	*Dicaeum eximium*	LC
	Emberizidae	*Atlapetes flaviceps**	EN
		*Atlapetes melanopsis**	EN
		*Atlapetes nationi**	LC
		Atlapetes pallidiceps	CR
		*Atlapetes terborghi**	NT
		*Emberiza koslowi**	NT
		*Incaspiza ortizi**	VU
		*Incaspiza watkinsi**	NT
		*Latoucheornis siemsseni**	LC
		Passerina rositae	NT
		Peucaea sumichrasti	NT
		Spizella wortheni	EN
		Sporophila melanops	CR
		*Torreornis inexpectata**	EN
	Estrildidae	*Lonchura caniceps*	LC
		Lonchura melaena	LC
		Lonchura monticola	LC
		Lonchura vana	VU
	Formicariidae	*Grallaria blakei**	NT
		Grallaria fenwickorum	CR
		*Grallaria przewalskii**	LC
		*Grallaricula lineifrons**	NT
		*Grallaricula ochraceifrons**	EN
		*Hylopezus auricularis**	VU
	Fringillidae	*Carduelis johannis**	EN
		*Carpodacus eos**	LC
		*Carpodacus roborowskii**	LC
		Leucosticte sillemi	DD
		*Rhynchostruthus louisae**	NT
		*Serinus rothschildi**	LC
		*Serinus xantholaemus**	VU
	Furnariidae	*Acrobatornis fonsecai**	VU
		*Cinclodes palliatus**	CR
		*Geositta crassirostris**	LC
		*Pseudasthenes cactorum**	LC
		*Siptornopsis hypochondriaca**	VU
		*Synallaxis beverlyae**	NT

		Synallaxis courseni	VU
		*Synallaxis kollari**	EN
		*Synallaxis zimmeri**	EN
		*Thripophaga berlepschi**	VU
		*Thripophaga cherriei**	VU
	Hirundinidae	*Eurochelidon sirintarae*	CR
	Icteridae	*Nesopsar nigerrimus**	EN
		*Sturnella defilippii**	VU
	Malaconotidae	*Laniarius amboimensis**	EN
	Melanocharitidae	*Melanocharis arfakiana*	DD
	Meliphagidae	*Anthornis melanura**	LC
		*Lichenostomus obscurus**	LC
		*Lichenostomus subfrenatus**	LC
		*Lichmera alboauricularis**	LC
		*Macgregoria pulchra**	VU
		*Melidectes belfordi**	LC
		Melidectes foersteri	LC
		*Melidectes fuscus**	LC
		*Melidectes leucostephes**	LC
		*Melidectes nouhuysi**	LC
		*Melidectes ochromelas**	LC
		Melidectes princeps	VU
		*Melidectes rufocrissalis**	LC
		*Melidectes torquatus**	LC
		Melidectes whitemanensis	NT
		*Melilestes megarhynchus**	LC
		*Meliphaga albonotata**	LC
		*Meliphaga aruensis**	LC
		*Meliphaga flavirictus**	LC
		*Meliphaga mimikae**	LC
		*Meliphaga montana**	LC
		*Meliphaga orientalis**	LC
		Melipotes ater	LC
		*Melipotes fumigatus**	LC
		*Melipotes gymnops**	LC
		*Myzomela adolphinae**	LC
		*Myzomela cruentata**	LC
		*Myzomela eques**	LC
		Myzomela erythromelas	LC
		Myzomela lafargei	LC
		*Myzomela rosenbergii**	LC
		Myzomela sclateri	LC
		*Notiomystis cincta**	VU
		*Oreornis chrysogenys**	LC
		*Philemon brassi**	NT
		Philemon cockerelli	LC
		*Philemon meyeri**	LC
		*Prosthemadera novaeseelandiae**	LC
		*Ptiloprora erythropleura**	LC
		Ptiloprora guisei	LC
		*Ptiloprora mayri**	LC
		*Ptiloprora meekiana**	LC
		*Ptiloprora perstriata**	LC
		*Ptiloprora plumbea**	LC
		*Pycnopygius cinereus**	LC
		*Pycnopygius ixoides**	LC
		Stresemannia bougainvillei	LC
		*Timeliopsis fulvigula**	LC
		*Timeliopsis griseigula**	LC
		*Xanthotis polygrammus**	LC
	Mimidae	*Toxostoma guttatum*	CR
	Monarchidae	*Monarcha erythrostictus*	LC
		*Monarcha loricatus**	LC
		*Monarcha pileatus**	LC
		Monarcha verticalis	LC
		Myiagra hebetior	LC
	Muscicapidae	*Cossypha heinrichi**	VU
		*Dioptrornis brunneus**	LC
		*Ficedula timorensis**	NT
		*Luscinia obscura**	VU
		*Luscinia pectardens**	NT

		*Luscinia ruficeps**	VU
		*Phoenicurus alaschanicus**	NT
		*Rhinomyias additus**	NT
		*Rhinomyias brunneatus**	VU
		*Sheppardia gabela**	EN
		*Xenocopsychus ansorgei**	NT
	Nectariniidae	*Aethopyga linaraborae**	NT
	Oriolidae	*Oriolus mellianus**	VU
	Pachycephalidae	*Pachycephala implicata*	LC
		Pachycephala leucogastra	LC
		Pachycephala modesta	LC
		*Pachycephala nudigula**	LC
	Paradisaeidae	*Astrapia mayeri*	NT
		Astrapia rothschildi	LC
		Astrapia stephaniae	LC
		Paradisaea guilielmi	NT
		Paradisaea raggiana	LC
		Paradisaea rudolphi	VU
		Parotia helenae	LC
		Parotia lawesii	LC
		Parotia wahnesi	VU
		Ptiloris intercedens	LC
	Paridae	*Parus davidi**	LC
		*Parus superciliosus**	LC
		*Parus venustulus**	LC
	Parulidae	*Dendroica angelae**	VU
		Geothlypis beldingi	CR
		Geothlypis speciosa	EN
		Vermivora bachmanii	CR
	Passeridae	*Montifringilla ruficollis**	LC
	Pipridae	*Antilophia bokermanni**	CR
		Lepidothrix vilasboasi	VU
	Pittidae	*Pitta anerythra*	VU
		*Pitta dohertyi**	NT
		*Pitta gurneyi**	EN
	Platysteiridae	*Batis minima**	NT
		*Platysteira laticincta**	EN
	Ploceidae	*Malimbus ibadanensis*	EN
		*Ploceus golandi**	EN
	Polioptilidae	*Polioptila clementsi**	CR
	Prunellidae	*Prunella fagani**	NT
	Ptilonorhynchidae	*Amblyornis subalaris*	LC
		Sericulus bakeri	NT
	Pycnonotidae	*Chlorocichla prigoginei**	EN
		*Phyllastrephus leucolepis**	CR
		*Pycnonotus hualon**	LC
	Rhinocryptidae	*Merulaxis stresemanni**	CR
		*Scytalopus griseicollis**	LC
		*Scytalopus iraiensis**	EN
		*Scytalopus robbinsi**	EN
		*Scytalopus rodriguezi**	EN
		*Scytalopus unicolor**	LC
	Rhipiduridae	*Rhipidura dahli*	LC
		Rhipidura drownei	LC
		*Rhipidura superflua**	LC
	Sittidae	*Sitta victoriae*	EN
		*Sitta yunnanensis**	NT
	Sturnidae	*Basilornis galeatus**	NT
	Sylviidae	*Bradypterus timorensis**	NT
		Cettia haddeni	NT
		*Macrosphenus pulitzeri**	EN
		Megalurulus grosvenori	VU
		Megalurulus llaneae	NT
		Megalurulus rubiginosus	LC
		Megalurulus whitneyi	NT
		*Phylloscopus claudiae**	LC
		*Phylloscopus emeiensis**	LC
		*Phylloscopus hainanus**	VU
		*Phylloscopus kansuensis**	LC
		*Phylloscopus yunnanensis**	LC
		*Seicercus omeiensis**	LC

		*Seicercus soror**	LC
	Thamnophilidae	*Herpsilochmus gentryi**	NT
		*Herpsilochmus parkeri**	EN
		*Myrmeciza castanea**	LC
		*Myrmoborus melanurus**	NT
		*Percnostola arenarum**	VU
		*Pithys castaneus**	NT
		*Pyriglena atra**	EN
		*Rhopornis ardesiacus**	EN
	Thraupidae	*Dacnis berlepschi**	VU
		*Dacnis hartlaubi**	VU
		*Diglossa gloriosissima**	EN
		*Euphonia concinna**	LC
		*Tangara meyerdeschauenseei**	VU
		*Tangara phillipsi**	NT
		*Wetmorethraupis sterrhopteron**	VU
	Timaliidae	*Alcippe cinereiceps**	LC
		*Alcippe ruficapilla**	LC
		*Alcippe striaticollis**	LC
		*Alcippe variegaticeps**	VU
		*Babax koslowi**	NT
		*Babax waddelli**	NT
		*Chrysomma poecilotis**	LC
		*Garrulax berthemyi**	LC
		*Garrulax bieti**	VU
		Garrulax courtoisi	CR
		*Garrulax davidi**	LC
		*Garrulax lunulatus**	LC
		*Garrulax sukatschewi**	VU
		*Liocichla bugunorum**	VU
		*Liocichla omeiensis**	VU
		Malacocincla perspicillata	DD
		*Paradoxornis conspicillatus**	LC
		*Paradoxornis paradoxus**	LC
		*Paradoxornis przewalskii**	VU
		*Paradoxornis zappeyi**	VU
		*Stachyris latistriata**	NT
		*Stachyris nonggangensis**	NT
	Troglodytidae	*Ferminia cerverai**	EN
		Hylorchilus navai	VU
		Hylorchilus sumichrasti	NT
		*Thryothorus griseus**	LC
	Turdidae	*Alethe choloensis**	EN
		*Turdus feae**	VU
		*Turdus helleri**	CR
		*Turdus kessleri**	LC
		*Turdus ludoviciae**	VU
		*Turdus mupinensis**	LC
		*Zoothera dumasi**	NT
		*Zoothera mendeni**	NT
		Zoothera talaseae	NT
	Tyrannidae	*Myiarchus semirufus**	EN
		*Poecilotriccus luluae**	VU
		Poecilotriccus senex	LC
		*Zimmerius villarejoi**	VU
	Urocynchramidae	*Urocynchramus pylzowi**	LC
	Zosteropidae	*Lophozosterops superciliaris**	LC
		*Madanga ruficollis**	EN
		*Zosterops buruensis**	LC
		Zosterops hypoxanthus	LC
		Zosterops metcalfii	LC
		Zosterops rendovae	LC
Piciformes	Picidae	*Campephilus imperialis*	CR
		Campephilus principalis	CR
		*Picumnus steindachneri**	VU
	Ramphastidae	*Megalaima faber**	LC
Psittaciformes	Psittacidae	*Amazona agilis**	VU
		*Amazona collaria**	VU
		Amazona viridigenalis	EN
		*Amazona vittata**	CR
		Anodorhynchus glaucus	CR

		Cacatua ophthalmica	VU
		Charmosyna diadema	CR
		Charmosyna meeki	NT
		Charmosyna rubrigularis	LC
		*Charmosyna toxopei**	CR
		*Cyanopsitta spixii**	CR
		*Forpus xanthops**	VU
		*Loriculus sclateri**	LC
		Loriculus tener	NT
		Lorius hypoinochrous	LC
		*Ognorhynchus icterotis**	EN
		*Prioniturus mada**	LC
		*Pyrrhura griseipectus**	CR
		*Pyrrhura orcesi**	EN
		Rhynchopsitta pachyrhyncha	EN
		*Tanygnathus gramineus**	VU
Strigiformes	Aegothelidae	*Aegotheles tatei*	DD
	Caprimulgidae	*Caprimulgus prigoginei**	EN
		Siphonorhis americana	CR
	Podargidae	*Rigidipenna inexpectata*	LC
	Strigidae	*Glaucidium sanchezi*	LC
		Nesasio solomonensis	VU
		Ninox odiosa	VU
		Ninox variegata	LC
		*Otus alfredi**	EN
		*Xenoglaux loweryi**	EN
	Tytonidae	*Phodilus prigoginei**	EN
		Tyto aurantia	VU
Tinamiformes	Tinamidae	*Crypturellus casiquiare**	LC
Trochiliformes	Trochilidae	*Aglaeactis aliciae**	EN
		Amazilia luciae	CR
		Campylopterus excellens	NT
		*Chlorostilbon olivaresi**	LC
		*Coeligena orina**	CR
		*Eriocnemis godini**	CR
		Eriocnemis isabellae	CR
		Eupherusa cyanophrys	EN
		Eupherusa poliocerca	VU
		*Heliangelus regalis**	EN
		Heliangelus zusii	DD
		*Loddigesia mirabilis**	EN
		Lophornis brachylophus	CR
		*Selasphorus ardens**	VU
		*Taphrolesbia griseiventris**	EN
		Thalurania ridgwayi	VU
Trogoniformes	Trogonidae	*Apalharpactes reinwardtii**	EN

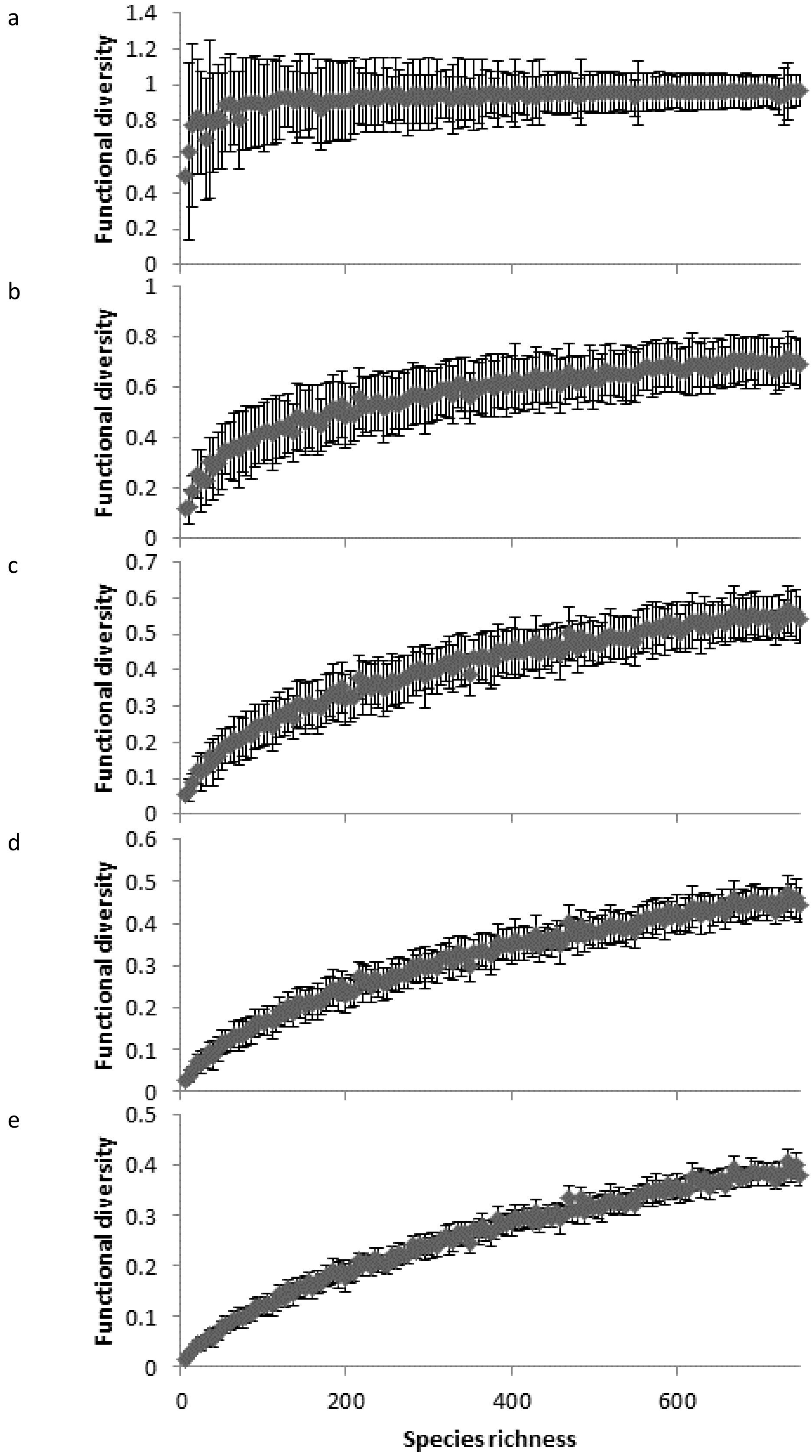
Appendix S10: Some methodological considerations addressed in the analysis of data for this thesis

Number of traits

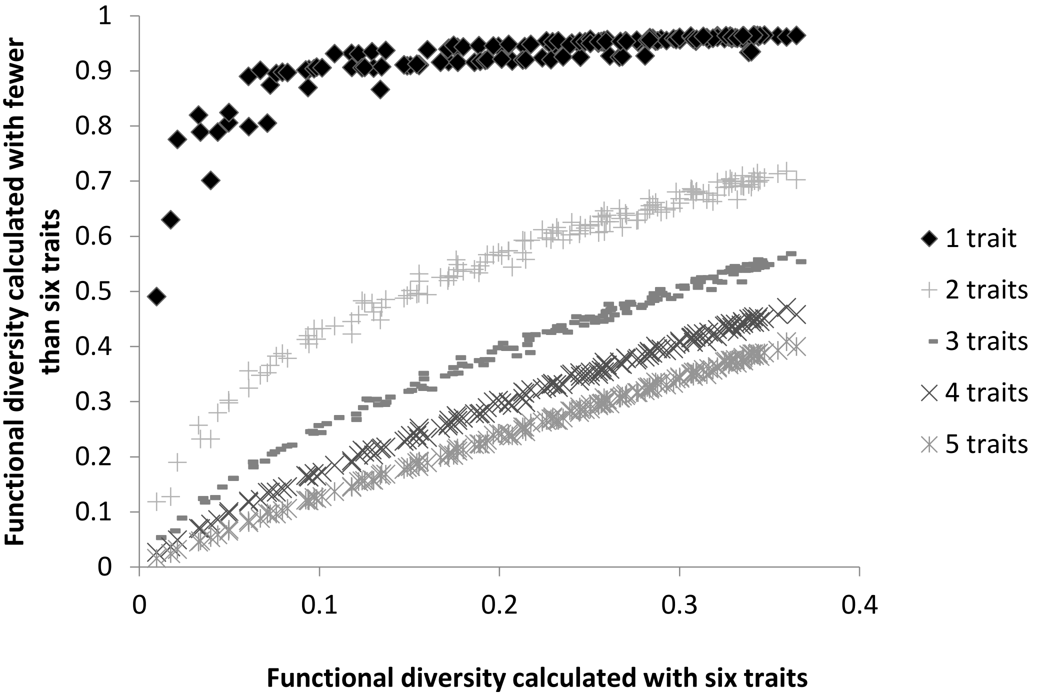
In order to test the effects of using fewer traits to calculate functional diversity, I used subsets of the traits to perform calculations. I used a dataset of 5,370 species from across the globe and then created a set of 150 randomly selected communities with species richness from 5 to 750.

As expected, when only one trait was used, functional diversity saturated at very low species richness (i.e. there was very high redundancy; Supplementary Figure 8). As more traits were used, redundancy became less apparent.

When functional diversity was calculated with just one trait, it showed a curvilinear relationship with functional diversity calculated with six traits (Supplementary Figure 9). The relationship between the two measures of functional diversity became more linear with the addition of more traits. In my analyses, I use six traits (expanded into 19 data points, e.g. the diet trait has six values associated with it; see Table 2.1). This suggests that the qualitative results and conclusions would not have been substantially different if fewer (or more) traits had been used to calculate FD.



Supplementary Figure 8: The relationship between species richness and functional diversity when the latter is calculated using (a) 1 trait, (b) 2 traits, (c) 3 traits, (d) 4 traits and (e) 5 traits.



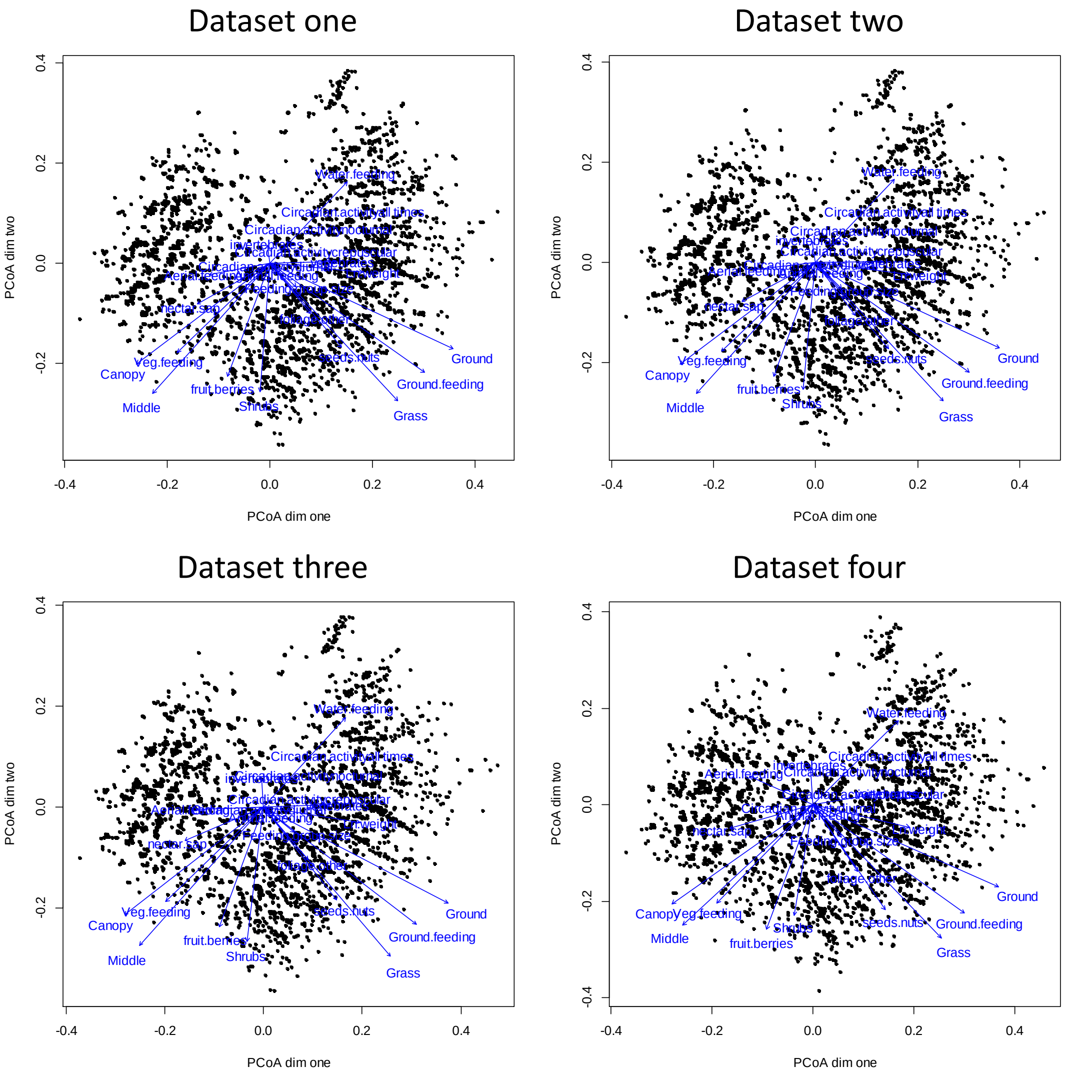
Supplementary Figure 9: The relationship between functional diversity calculated using six traits (as is the method in this thesis) and functional diversity calculated using fewer than six traits.

Data quality

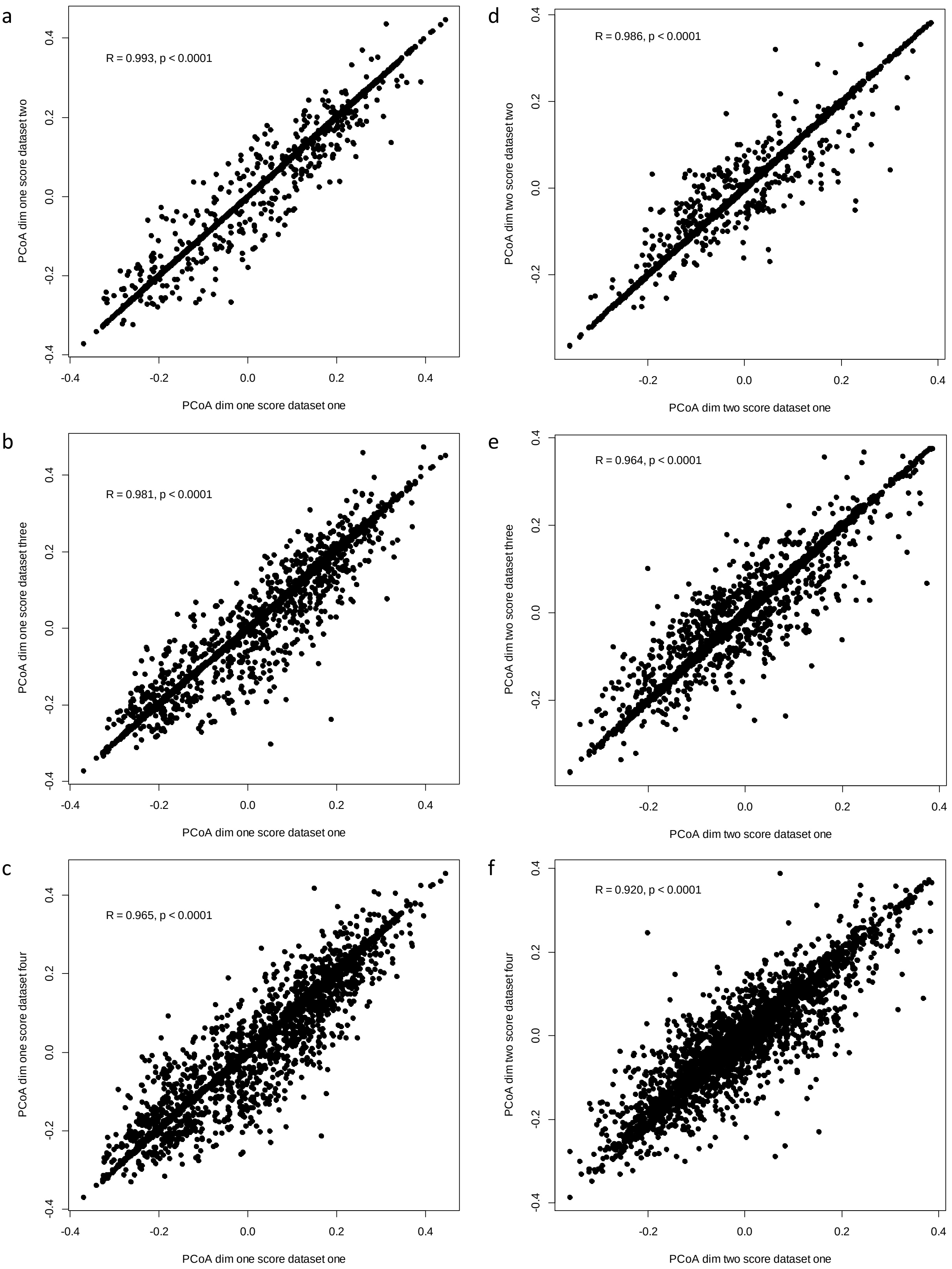
In order to test the robustness of the analyses to the quality of the data, I performed some sensitivity analyses. I used a dataset of 5,370 species from across the globe for which I had a complete set of trait data for at least two members of the genus (so that generic values could be calculated) and the same randomly selected communities as in the previous analysis. I performed a PCoA analysis to ordinate the species in multidimensional trait space. The trait vectors and factors were fitted to the first two dimensions of the PCoA to identify which functional traits were most important in differentiating between species. I then calculated the mean value of the first two PCoA dimensions and functional richness for the 150 randomly selected communities.

I then compared the results using this first dataset with those obtained using datasets which increasingly relied on genus and family values. For the second dataset, I randomly selected 4% of the species trait data to be replaced with genus values, and an additional 1% to be replaced with family values. The third dataset used 10% genus values and 2.5% family values, and the fourth dataset used 20% genus values and 5% family values.

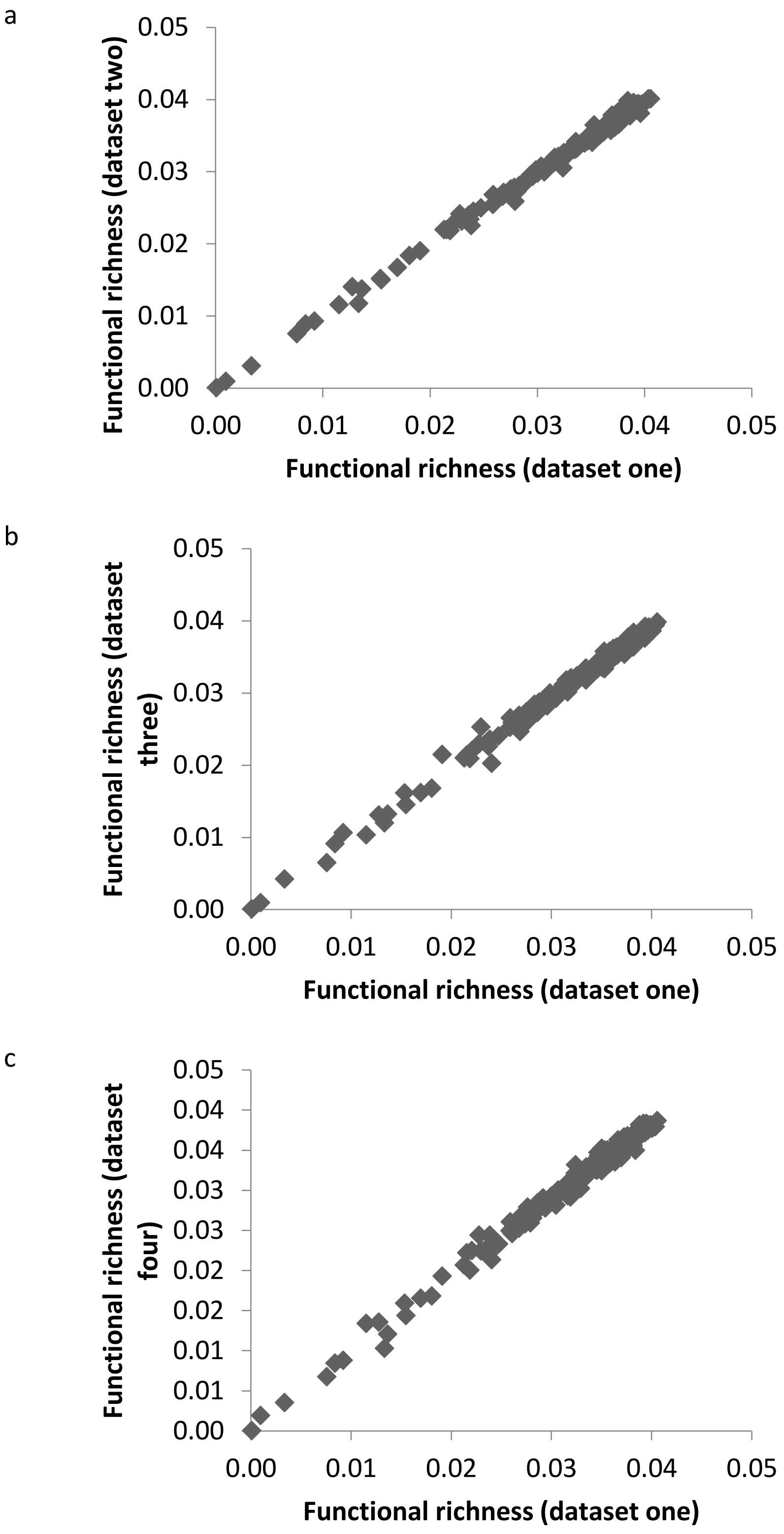
The distribution of species in trait space looked very similar using each of the four datasets and the same traits loaded onto the first two PCoA dimensions (Supplementary Figure 10). The mean value of dimensions one and two calculated using dataset one (i.e. the true values) was highly correlated with the values calculated using datasets two, three and four (Supplementary Figure 11). Even when only 75% of the trait values were true species values, there was very high correlation with the true values (r=0.965 for dimension one and r=0.920 for dimension two). Correlations with mean values of dimensions three and four were also calculated and the results were highly similar, so they are not reported. There was also very high correlation between functional richness calculated using dataset one and each of the three other datasets (Supplementary Figure 12). A similar result was obtained when functional diversity was calculated using a dendrogram for each of the four datasets.



Supplementary Figure 10: Dimensions one and two of the Principal Coordinates Analysis (PCoA) calculated using each of the four datasets. Each point is one species in functional trait space.



Supplementary Figure 11: The correlations between the mean PCoA scores for dimension 1 (a-c) and 2 (d-f) when calculated using dataset one compared to dataset two (a,d), dataset three (b,e) and dataset four (c,f).



Supplementary Figure 12: The correlations between functional richness calculated using dataset one and (a) dataset two (r=0.998), (b) dataset 3 (r=0.996) and (c) dataset four (r=0.995). All are significant at p<0.0001.

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